Verzuring van vennen: een tijdsverschijnsel

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VERZURING VAN VENNEN: EEN TIJDSVERSCHIJNSEL

Proefschrift
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ABSTRACT

Van Dam, H. (1987) Acidification of moorland pools: a process in time. Doctoral thesis, Wageningen, 175 p.

Changes in chemistry, particularly pH, of a number of soft-water moorland pools in The Netherlands are described. Several groups of organisms, including diatoms, and direct measurements are used to infer past pH values. Diatoms were studied from preserved samples from the beginning of the 20th century, from recent samples and from sediment cores. Old data about chemistry, macrophytes and human impact were obtained from published and unpublished documents.

In isolated pools in nature reserves the pH declined to c. 4 from initial values between 4 and 6 at the beginning of this century. Small inputs of nutrients by agriculture, fisheries or swimming retards acidification. The diversity and dissimilarity of diatom assemblages decrease by acidification, particularly in clear water pools. Acidification boosts the growth of the diatom Eunotia exigua.

Sulphate concentrations were extremely high in 1977 and 1978 in two clear water pools where more than half of the bottom surface was exposed to the atmosphere during the extremely dry summer of 1976 and decreased afterwards, parallel to Juncus bulbosus. E. exigua decreased with a delay. Apparently reduced sulphur compounds, which accumulated in the bottom due to atmospheric deposition in the decades before, were oxidized in the dry summer of 1976. No such changes were seen after the dry summer of 1921. In these two pools the pH declined from 5-6 in 1920 to c. 4 in c. 1980. In a brown water pool, where only a small fraction of the bottom was exposed in 1976, changes by the drought were small. Also the decline of pH in this pool since 1920 (c. 0.5 unit) was relatively small.

Palaeolimnological studies were conducted in three pools, which were supposed to be pristine. However, it appeared both from coring results and documented evidence that these pools had pH values between 4 and 5 in the early 19th century and became subsequently more alkaline by nutrient enrichment. After 1900 the pools were acidified because anthropogenic enrichment was finished and acid atmospheric deposition increased.

To follow the effect of future changes of acid atmospheric deposition and understand the processes involved, chemical and biological monitoring should continue. Input of buffering substances in some moorland pools could maintain weakly acid conditions in Dutch surface waters.

Stellingen

1. Een goed ven behoort op de wind te liggen.

2. Het komen en gaan van vissen en waterplanten met rozetvormige groeiwijze in Nederlandse vennen is voor een belangrijk deel een cultuurverschijnsel.

3. Natuurlijkheid is geen geschikt criterium om wateren te beoordelen.

   Rijkswaterstaat (1986). De waterkwaliteit van Nederland, indicatief meerjarenprogramma water 1985-1989. Staatsdrukkerij, 's-Gravenhage.

4. Patrick e.a. vatten de soortabundantieverdeling van kiezelwierencombinaties ten onrechte samen in een log-normale verdelingskromme.

   R. Patrick, M.H. Hohn & J.H. Wallace (1954). Notulae Naturae, Academy of Natural Sciences, Philadelphia 416: 1-16.
   H. van Dam (1982). Nova Hedwigia/Beiheft 73: 97-115.

5. De kwantitatieve vermindering van het taxonomisch onderzoek aan zoetwaterorganismen belemmert de vooruitgang van biologische waterbeoordeling.

6. Frequente veranderingen in nomenclatuur en taxonomie van zoetwaterorganismen belemmeren de vooruitgang van biologische waterbeoordeling eveneens.

7. Indien biologen criteria voor de beoordeling van waterkwaliteit op grond van het planktonbestand duidelijk formuleren, zijn analisten uitstekend in staat deze beoordeling uit te voeren.

   P.F.M. Coesel (1981). Distribution and ecology of desmids in a Dutch broads area. Proefschrift, Universiteit van Amsterdam.

8. Het maatschappelijk effect van biologische monitoring moet niet worden overschat: biologische signalen van negatieve milieuveranderingen worden nu ook genegeerd of onvoldoende serieus genomen.

   W.J. ter Keurs & E. Meelis (1986). Environmental Monitoring and Assessment 7: 161-168.

9. Privatisering van het beheer van natuurgebieden zal de collectieve waarden van deze terreinen benadelen.

10. Leven is een grensvlakverschijnsel, goed leven een tijdsverschijnsel.

Herman van Dam
Verzuring van vennen: een tijdsverschijnsel
Wageningen, 27 mei 1987

INHOUD

De auteur is veel dank verschuldigd aan iedereen die hem het werken aan dit proefschrift mogelijk heeft gemaakt.

Het Van Tienhoven Studiefonds verleende een bijdrage in de drukkosten.

HOOFDSTUK 1

INLEIDING

Motivering en doelstelling

Bij de aanvang van dit onderzoek, in 1976, was over de invloed van zure neerslag* op Nederlandse oppervlaktewateren nauwelijks iets bekend. In gebieden met een veel geringere atmosferische zure depositie dan in ons land, zoals Scandinavië (OECD 1977, EMEP-CCC 1984), loopt de visstand van kalkarme, slecht gebufferde wateren al sinds de jaren twintig terug als gevolg van verzuring van het oppervlaktewater door zure neerslag (b.v. Almer e.a. 1974, Braekke 1976)

Schadelijke invloeden van zure atmosferische depositie op bomen en daarop levende korstmossen zijn in dichtbevolkte en geïndustrialiseerde gebieden al meer dan honderd jaar bekend (Nylander 1866, Von Schroeder 1873). Barkman (1958) en De Wit (1976) toonden aan dat de korstmossenflora op Nederlandse bomen door de invloed van zure neerslag sterk is verarmd.

Daarom werd verwacht dat verzuring van kalkarme, slecht gebufferde wateren ook hier vastgesteld zou kunnen worden. Tot deze wateren behoren voornamelijk vennen en kalkarme duinmeren. Vennen zijn van oorsprong voedselarme plassen op pleistocene, kalkarme zandgrond, met een wisselende waterstand (Figuur 1). Doordat deze geheel of grotendeels door de neerslag van water worden voorzien, is de chemische samenstelling van het venwater erg gevoelig voor antropogene beïnvloeding. Veel vennen hebben dan ook hun oorspronkelijke karakter verloren na bemesting met landbouwwater, visserij, zwemmen enz. Uit een oriënterende studie bleek dat geïsoleerde vennen in Noord-Brabant en op de Veluwe tussen ca 1920 en ca 1975 waren verzuurd (Van Dam 1978).

Voedselarme, en in het bijzonder matig voedselarme, vennen herbergen karakteristieke levensgemeenschappen en behoren tot de meest waardevolle natuurelementen van ons land. Omdat dergelijke wateren in de ons omringende landen veel minder algemeen voorkomen, zijn de Nederlandse vennen ook internationaal van betekenis. Betrekkelijk ongestoorde vennen zijn zeldzaam en komen bijna alleen nog in natuurreservaten voor (Westhoff e.a. 1970, Dierssen 1972, 1975, Schroevers 1979, Westhoff 1979, Coenen 1981).

Teneinde gegevens te kunnen verschaffen, die nodig zijn voor het voeren van een doeltreffend beleid met betrekking tot de bestrijding van verzuring, was systematische studie van de invloed van zure neerslag op vennen wenselijk.

Verzuring is een tijdsverschijnsel, in de dubbele betekenis van het woord. Daarom moet het proces ook in de tijd worden gevolgd. Wanneer een verzuurd ven als een onwenselijke toestand wordt beschouwd, is het voor een juiste beoordeling van die toestand nodig te weten hoe een 'normaal' of 'typisch' ven eruitziet. De concepten 'normaal' of 'typisch' zijn moeilijk te definiëren en hebben weinig betekenis zonder lange-termijngegevens. Ecologische analyses of interpretaties die op korte-termijngegevens (1-3 jaar) zijn gebaseerd, kunnen zeer misleidend zijn. Lange-termijn veranderingen zijn vaak geleidelijk en subtiel, maar worden dikwijls overschaduwd door uitzonderlijke gebeurtenissen, die zich gedurende een korte periode voordoen. Hierdoor is het moeilijk om te beoordelen of een

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*De term zure neerslag wordt hier en verder gebruikt voor (potentieel) verzurende natte en droge depositie.

Fig. 1. Verspreiding van de 900 vennen, betrokken bij het onderzoek van de Stichting Onderzoek Levensgemeenschappen, 1957-1959 (P.J. Schroevers, ongepubliceerd).

waargenomen verandering een trend of natuurlijke fluctuatie is (Likens 1983, 1984).

Naast zure neerslag beïnvloeden ook andere factoren de chemie van vennen, hetgeen o.a. blijkt uit de grote verschillen in zuurgraad tussen vennen, met name in het verleden (Kersten 1985).

Ontwikkelingen in het botanisch onderzoek van vennen

De opzet van dit onderzoek is in sterke mate bepaald door de resultaten van vroegere botanische onderzoekingen van vennen. Om de lezer in staat te stellen dit onderzoek in een historisch en eigentijds referentiekader te plaatsen, geeft het volgende een overzicht van ontwikkelingen in het botanisch onderzoek van Nederlandse vennen, zonder dat naar volledigheid is gestreefd. Af en toe worden deze in de context van het onderzoek in de buurlanden geplaatst. De schaarse en weinig systematisch verzamelde waarnemingen uit de negentiende eeuw worden besproken door Heimans (1925) en Beijerinck (1926). Behalve voor de provincie Noord-Brabant (Mol 1986) bestaat er vooralsnog geen bibliografie van botanische literatuur over vennen. In de overzichten van Dresscher (1976a,b) zijn verwijzingen naar algologische literatuur over vennen opgenomen.

Ca 1900 - ca 1940

De studies uit deze periode werden verricht door individuele onderzoekers en hadden een zuiver wetenschappelijke doel. Hoewel de onderzoekers een sterke belangstelling hadden voor de betrekkingen tussen de organismen en hun milieufactoren, beschikten zij niet over de faciliteiten om regelmatig uitgebreide chemische analyses te verrichten. Hierdoor konden zij deze betrekkingen slechts in algemene termen aanduiden.

In aansluiting op soortgelijke studies in kalkarme, stilstaande wateren in het Zwarte Woud, door destijds vooraanstaande algologen als Schmidle (1893) en Rabanus (1915), onderzocht Heimans (1925) sieralgen (Desmidiaceae) uit 21 vennen bij Oisterwijk. Hij vond grote floristische verschillen tussen het oostelijk en het westelijk deel van dit gebied. Al tijdens zijn waarnemingsperiode (1919-1925) nam hij een voortdurende verarming van de aanvankelijk zeer rijke en bijzondere flora van de Centrale Vennen (in het westelijk deel) waar. Hij vermoedde dat kleine hydrologische veranderingen in het gebied hier debet aan waren.

Beijerinck (1926) bestudeerde de verspreiding en seizoenperiodiciteit van zoetwaterwieren uit ongeveer 200 vennen in Zuidwest-Drente. Naar de voorkomende soorten macrofyten verdeelde hij de vennen in drie groepen, waarvan de wierengemeenschappen door verschillende gidssoorten werden gekenmerkt. De mesotrofe (matig voedselrijke) en oligo-mesotrofe (matig voedselarme) groep komen ongeveer overeen met de flora van respectievelijk de westelijke en oostelijke vennengroep van Heimans (1925). De derde groep omvatte zeer voedselarme, ondiepe heiplassen en hoogveenpoelen.

Het werk van Heimans en Beijerinck kon zich meten met het buitenlandse onderzoek op dit terrein. Donat (1926) vond een verarming van de sieralgenflora in Noordduitse laag-alkaliene wateren door voedselverrijking. Dobers (1929) deelde als een der eersten algesoorten in naar het pH-traject waarin zij voorkomen. Budde (1942) vond een nauwe relatie tussen de pH en het voorkomen van algesoorten in een complex van vennen en kalkarme meren bij Münster. In België werd de relatie tussen pH en het voorkomen van sieralgen onderzocht door Van Oye (1935) en Van Oye & Cornil (1941). Het grootste aantal soorten werd bij een pH tussen 5,5 en 6,8 aangetroffen. Verschillende van deze onderzoekers realiseerden zich daarbij dat niet alleen de pH, maar ook andere factoren het voorkomen van algesoorten bepalen, zodat bij een zelfde pH soms verschillende algengemeenschappen kunnen voorkomen.

In tegenstelling tot het microfytenonderzoek liep het Nederlandse macrofytenonderzoek in kalkarme (en ook andere) wateren sterk achter op dat in het buitenland. Terwijl b.v. Wirtgen (1865) reeds uitvoerig de vegetatie

van Eifelmaaren beschreef, Pearsall (1920) de relatie tussen aquatische macrofyten en bodemsamenstelling in het Engelse Lake District onderzocht en Iversen (1929) rapporteerde over de relatie tussen pH en macrofyten in Deense meren, duurde het tot 1933 eer Van de Griendt op systematische wijze de water- en moerasplanten van 13 vennen bij Oisterwijk inventariseerde. In samenhang met de voedselrijkdom van het water onderscheidde hij een zevental vegetatietypen, waarbij hij een positief verband tussen het aantal soorten en de mate van voedselrijkdom constateerde. Beijerinck (1936) gaf een globale indeling van vegetatietypen van vennen op de Dwingeloosche Heide in relatie tot voedselrijkdom, humusgehalte en diepte van het water.

In tijdschriften voor natuurliefhebbers werden in verschillende bijdragen aspecten van de plantengroei van vennen belicht. Beijerinck (1933) ging in op bouw, verwantschap en verspreiding van veenmossen en classificeerde de soorten naar de zuurgraad en de mate van voedselrijkdom waarbij zij voorkomen. Globale beschrijvingen, b.v. Thijsse (1915, 1916, 1929), Beijerinck (1924), Sloff (1928) en Van Vroonhoven (1935), ontsloten de botanische rijkdommen van gerenommeerde vennengebieden voor een groter publiek. Voor een aantal vennen is het mogelijk om met behulp van deze beschrijvingen, eventueel aangevuld met ongepubliceerde floristische gegevens, oude foto's en herbariumvondsten, achteraf een tamelijk volledig beeld van de toenmalige macrofytenvegetatie te schetsen, zoals in Lemaire (1977), Van Dam (1983) en Hoofdstuk 4 van dit proefschrift. Over de meeste Nederlandse vennen bestaan uit deze periode echter geen publikaties of rapporten. Soms is herbariummateriaal beschikbaar, dat verzameld is in het kader van de plantengeografische kartering van Nederland (Mennema e.a. 1980, 1985).

Ca 1940 - ca 1970

In deze periode vindt het onderzoek op meer georganiseerde wijze plaats dan in de vorige periode, waardoor er meer sprake is van teamwork. Hoewel zuiver wetenschappelijke motieven nog steeds een rol blijven spelen, richt het onderzoek zich steeds meer op natuurbehoud en -beheer. Dit hangt samen met de sterke biologische verarming van de voedselarme componenten van het landschap als gevolg van agrarische en industriële ontwikkelingen. Vooral aan het eind van dit tijdperk worden uitvoerige fysische en chemische metingen aan de onderzochte vennen verricht, waardoor een correlatieve analyse van de relaties tussen organismen en hun milieufactoren mogelijk wordt.

In 1942 stelde de Nederlandsche Natuurhistorische Vereeniging de Commissie voor het Onderzoek der Vennen in, met als taak een vergelijkende limnologische studie te maken van vennen, venen, poelen en plassen in Nederland. C. van Rijsinge fungeerde als voorzitter en J.G. Sloff als secretaris-penningmeester. In 1943 werd een werkkamp te Boxtel gehouden en vorm en diepte van enkele vennen werden opgemeten. Na enkele jaren werd de Commissie opgeheven. De leden publiceerden globale beschrijvingen van enkele vennen (b.v. Margadant & Van der Wijk 1942), terwijl van het Groot Huisven een uitvoerige vegetatiebeschrijving verscheen (Mörzer Bruijns e.a. 1943).

Van Heusden & Meijer (1949) gaven uitgebreide lijsten van mossen en vaatplanten, vegetatiebeschrijvingen en enkele chemische eigenschappen, waaronder pH en alkaliniteit, van 45 vennen uit verschillende provincies. De samenstelling van de mossenflora hing nauw samen met pH en voedselrijkdom (Meijer 1958).

Bij het onderzoek in de Oisterwijkse vennen, onder auspiciën van de Hydrobiologische Vereniging (H.V.) , werden de effecten van interne beheersmaatregelen gevolgd. Van Dijk e.a. (1948) inventariseerden flora en

vegetatie van het Goorvennencomplex bij Oisterwijk. In het Voorste Goorven en daarmee in verbinding staande vennen kwamen plantesoorten uit een zeer voedselrijk milieu voor, waarvan de aanwezigheid werd toegeschreven aan lozing van afvalwater door een café. Op grond van onderzoekbevindingen werd de lozing gestaakt en de modderlaag werd uit de vennen verwijderd. Na de schoonmaak keerden enkele hogere planten uit matig voedselrijk milieu terug, bij de sieralgen was dit niet het geval (Van Dijk & Westhoff 1960, Heimans 1960).

De H.V. organiseerde eveneens de inventarisatie van flora en fauna van de Gerritsfles bij Kootwijk (Dresscher e.a. 1952). In vergelijking met 1918 was het aantal soorten sieralgen achteruitgegaan, hetgeen als verzuring werd geïnterpreteerd. De basisgegevens van dit onderzoek zijn deels vastgelegd in een randponskaartensysteem, dat door de H.V. werd opgezet en nog in het archief van deze vereniging aanwezig is. Het plan om in dit systeem alle biologische en chemische waarnemingen aan Nederlandse wateren vast te leggen bleek te ambitieus en moest na enkele jaren worden verlaten.

Wartena (1954) onderzocht sieralgen van 56 Drentse vennen. Zij vond een vermindering van het aantal soorten in vergelijking met het onderzoek van Beijerinck (1926), maar kon de precieze oorzaak hiervan niet aangeven.

Zeven biologen, in dienst van de Stichting voor Onderzoek van Levensgemeenschappen (S.O.L), inventariseerden van 1957 tot 1959 de plantengroei van ca 900 vennen in heel Nederland. Het onderzoek had tot doel de onderzochte vennen in een aantal typen in te delen, als basis voor het aankoopbeleid van natuurgebieden. Een globale beschrijving van de vegetatie van elk ven, al of niet vergezeld van vegetatieopnamen, werd neergelegd in een excursieverslag. De pH-metingen, die met indicatorpapier in veel vennen werden verricht, zijn onbruikbaar. In zwak gebufferd water wordt zo altijd een pH van ca 5,4 gemeten (H.K.M. Moller Pillot, pers. meded.).

Er verschenen enkele publikaties over bijzondere vennen en zeldzame plantesoorten (o.a. Van Donselaar 1958, Van der Voo 1965), terwijl Van der Voo (1962) het verband tussen het voorkomen van vegetatietypen en menselijk handelen in een vijftigtal Twentse vennen samenvatte. Uit het onderzoek bleek dat de botanische kwaliteiten van de meeste onderzochte vennen in sterke mate negatief door menselijke activiteiten, o.a. ontwatering en bemesting, werden beïnvloed, evenals in Noord-Duitsland (Tüxen 1958). De botanisch rijkste vennen waren niet altijd degene die het minst door de mens waren beïnvloed. Zo kan gedeeltelijke verwijdering van het sediment de ontwikkeling van zeldzame planten bevorderen (Westhoff & Van Leeuwen 1959). Een samenvattende publikatie van het omvangrijke onderzoek bleef achterwege.

P. Leentvaar legde de planktonanalyses van enkele tientallen vennen vast in excursierapporten. Hij introduceerde het begrip metatrofie, dat een kunstmatig overgangsstadium tussen oligotrofie en eutrofie aangeeft; terwijl mesotrofie geen overgangsstadium, maar een permanente toestand is, die bijvoorbeeld door de chemische samenstelling van de bodem in stand gehouden wordt (Leentvaar 1958). Hoewel deze auteur geen kensoorten voor metatrofe wateren kon aanwijzen (er werd een combinatie van oligo- en eutrafente planktonsoorten aangetroffen), meent Schroevers (1962) dat deze wel bestaan.

Geelen (1969) bestudeerde maandelijks de kwalitatieve en kwantitatieve samenstelling van plankton in twee vennen bij Hatert, over een periode van drie jaar. In een voedselarm ven trof zij een fytoplanktongemeenschap van het goudwiertype aan. In een ven dat door landbouwwater en kokmeeuwen werd verontreinigd, kwam het groenwiertype voor. In het laatste ven was de biomassa van het fytoplankton acht maal zo hoog als in het eerste ven. Deze verschillen kwamen overeen met die welke Leentvaar (1967) in wel en niet door meeuwen verontreinigde vennen bij Hilversum en Leersum aantrof.

Ca 1970 - 1986

Meer dan in de vorige perioden vindt het onderzoek aan universiteiten plaats. Hoewel het academisch onderzoek vaak zuiver wetenschappelijk is, heeft het vaak een maatschappelijke motivering en richt het zich rechtstreeks op problemen die voortvloeien uit ontwikkelingen in de maatschappij. Mestoverschotten en zure neerslag hebben sterke invloeden op chemie en biologie van de zwak gebufferde wateren, die worden beschreven door vergelijking van inventarisatiegegevens met die uit de vorige perioden. Met de computer is het mogelijk geavanceerde statistische verwerkingsmethoden toe te passen op grote gegevensbestanden. Relaties tussen planten en hun milieu worden niet alleen door correlatieve analyse van de mate van voorkomen in het veld met aldaar gemeten omgevingskenmerken opgespoord, maar ook met causale analyse door middel van kweekexperimenten in het laboratorium.

Schoof-van Pelt (1973) bestudeerde de onderverdeling in gemeenschappen van het oeverkruidverbond* op enkele honderden plaatsen in Nederland, Frankrijk, Groot-Brittannië en Ierland. Daarbij werden ook ongepubliceerde opnamen uit vennen van W. Diemont en S. Sissingh uit 1936-43 en van het S.O.L.-onderzoek uit 1957-59 betrokken. Vooral associaties uit matig voedselarme en matig voedselrijke vennen, o.a. de Biesvaren-Waterlobelia-associatie, waren door ontwatering en voedselverrijking sterk achteruit gegaan. De vegetaties van de meest geïsoleerde vennen waren het minst veranderd.

Strijbosch (1976) typeerde de vegetatie van 27 vennen bij Hatert. Hij onderscheidde aan de hand van vegetatie en chemie drie typen: 'ongestoorde' vennen, door kapmeeuwen bemeste vennen en door agrarische activiteiten met mineralen verrijkte vennen.

Negatieve effecten van voedselverrijking op venvegetaties werden ook elders in Nederland, België, Westfalen en Nedersaksen geconstateerd (b.v. Lübben 1973, De Blust 1977, Dierssen 1973, Wittig 1980, Helming e.a. 1984).

Coesel & Smit (1977) onderzochten sieralgen uit Drentse vennen, waarvan een dertigtal door Beijerinck (1926) en Wartena (1954) was onderzocht. In vijftig jaar was het aantal soorten met de helft verminderd. Ten gevolge van voedselverrijking waren vooral soorten uit matig voedselrijke milieus achteruitgegaan. In voedselarme plassen waren zeldzame soorten verdwenen.

Coesel e.a. (1978) inventariseerden sieralgen in vennen bij Oisterwijk, waarvan er 15 eerder door Heimans (1925, 1960) werden onderzocht. In de 4 best onderzochte vennen kwamen in 1916-25 195 soorten voor, in 1975 nog slechts 68. Evenals in Drente waren vooral soorten uit matig voedselrijke milieus verdwenen door invloeden van landbouw, visserij etc. De sterke achteruitgang van sieralgen door voedselverrijking van oorspronkelijk voedselarme tot matig voedselrijke wateren is alom in Noordwest-Europa waargenomen (b.v. Förster 1970). In enkele geïsoleerde vennen vonden Coesel e.a. (1978) een achteruitgang van zeldzame soorten door verzuring.

De Vries (1984) onderzocht verschillen tussen kiezelwierencombinaties van het open water en van veenmosverlandingszones van Drentse vennen. Notenboom-Ram (1976) gebruikte een inventarisatie van kiezelwieren uit 46 Veluwse vennen voor een indeling van de onderzochte wateren naar voedselrijkdom en hydrobiologische waarde, die zij van de meeste locaties groot tot zeer groot achtte. De biologische waarde van vennen bij Turnhout, die door landbouw en

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*Nederlandse namen van plantengemeenschappen en plantesoorten in dit Hoofdstuk en Hoofdstuk 7 zijn in overeenstemming met respectievelijk Westhoff & Den Held (1969) en Van der Meijden e.a. (1983).

recreatie met voedingsstoffen werden verrijkt, was lager dan die van ongestoorde vennen in hetzelfde gebied, zoals Caljon (1975) door middel van fytoplanktonanalyse vaststelde.

Biere e.a. (1983) onderzochten aantallen hogere plantesoorten in betrekkelijk ongestoorde Drentse vennen. Het aantal soorten nam toe met de venoppervlakte en af met toenemende isolatie (afstand tot andere vennen), overeenstemmend met de verwachting.

Het verdwijnen van soorten van het oeverkruidverbond uit Oisterwijkse vennen door verzuring bleek in 1978 uit de publikatie van Hoofdstuk 2 van dit proefschrift. Roelofs (1983) en Arts e.a. (1986) vonden dat in ca 60% van de onderzochte laag-alkaliene wateren in verschillende provincies (voornamelijk vennen) waar na 1950 nog waterplanten met rozetvormige groeiwijze (biesvaren, oeverkruid en waterlobelia) voorkwamen; deze waren verdwenen ten gunste van knolrus en veenmos. Arts (1986) geeft een uitvoerig overzicht van de achteruitgang van soorten uit het oeverkruidverbond. Uit laboratoriumexperimenten bleek dat deze veranderingen te maken hebben met de koolstof- en stikstofhuishouding van genoemde soorten (Roelofs e.a. 1984, Schuurkes e.a., 1986).

Higler (1979) deed verslag van een nieuwe multidisciplinaire studie van de Gerritsfles bij Kootwijk. Directe metingen van de pH en veranderingen in de micro- en macroflora gaven aan dat het verzuringsproces zich sinds 1950 had voortgezet. Van Dam & Beljaars (1984) constateerden een sterke verzuring van Belgische en Duitse vennen, aan de hand van kiezelwieranalyses. Geelen & Leuven (1986) vonden in 35 laag-alkaliene wateren (pH 3.7 - 10.4) de geringste diversiteit van fytoplanktonsoorten in de meest zure wateren.

Opzet van het onderzoek

De lange voorgeschiedenis van dit proefschrift geldt niet alleen de tijdsperiode van ten minste enkele honderden jaren die wordt beschreven, maar ook de wording van het boekje zelf.

De aanleiding tot het onderzoek, waarmee in 1976 werd begonnen, was de participatie in de 'Landinrichtingsstudie Midden-Brabant' (Harms & Kalkhoven 1979, Werkgroep Methodologie 1983). Om de effecten van menselijke beïnvloeding op aquatische levensgemeenschappen aan te geven werd de recente hydrobiologische toestand van beken en vennen vastgelegd en vergeleken met de vroegere toestand (Van Dam 1979, 1983).

De biologische hoedanigheid van de vennen werd getypeerd met behulp van planktonmonsters uit de periode 1916-1929, die in verband met onderzoek van Heimans (1925, 1960) aan sieralgen (Desmidiaceae) werden genomen en zorgvuldig zijn bewaard, en planktonmonsters uit 1975. Uit de monsters werden kiezelwieren (Bacillariophyceae of Diatomeae) bestudeerd, omdat deze eencellige algen (microfyten) goede indicatoren zijn voor tal van milieuvariabelen, met name de zuurgraad (pH) van het water (Hustedt 1939, Cholnoky 1968, Meriläinen 1967, Kalbe 1973). De recente vegetatie van hogere water- en moerasplanten (macrofyten) werd vergeleken met oude gegevens. De biologische veranderingen werden gerelateerd aan veranderingen die in hydrologie, landbouw en recreatie hadden plaatsgevonden.

Een aantal vennen bleek verrijkt te zijn met voedingsstoffen door toevoer van water van landbouwpercelen, bemesting ten behoeve van de visstand of door excretieprodukten van badgasten. De macro- en microflora van geïsoleerde vennen, gevrijwaard van dergelijke storende invloeden, bleken te zijn verarmd door verzuring (zie ook Coesel e.a. 1978). Soorten die in West-Europa zeldzaam zijn, waren verdwenen ten gunste van algemene soorten. Dit onderzoek (Hoofdstuk 2) was een van de eerste studies waarin de

schadelijke gevolgen van zure neerslag werden vastgesteld buiten Scandinavïe en Noord-Amerika.

Suurmond (1980) inventariseerde kiezelwieren in monsters die rond 1920 en in 1978 werden genomen uit 16 vennnen bij Oisterwijk, Kootwijk en Dwingeloo. Daar verzuring door atmosferische depositie niet rechtstreeks is aan te tonen, maar slechts als 'restverklaring' overblijft na eliminatie van andere verstorende invloeden, werden slechts locaties gekozen, waarvan niet bekend was dat er andere verstorende beïnvloedingen hadden plaatsgevonden. Ook de Veluwse en Drentse vennen bleken verzuurd, maar de humeuze Drentse vennen in mindere mate dan de overige (Hoofdstuk 3). Verschillen in de mate van verzuring van niet-humeuze vennen werden toegeschreven aan variaties in gevoeligheid voor droogte (waterdiepte) en in de mate van bebossing rond de vennen. Bij contact tussen venwater en grondwater wordt het venwater verrijkt met zwavelverbindingen, die zich als gevolg van de hoge droge depositie van zwaveldioxide in (naald)bossen in het grondwater van de zandgebieden ophopen (Kemmers & Jansen 1980, Oosterom 1982, Stuyfzand 1984).

Het doel van het onderzoek dat in Hoofdstuk 4 wordt beschreven is om de invloeden van waterdiepte en droge perioden op verzuring van vennen te beschrijven. Analyses van planktonmonsters, genomen rond de extreem droge zomers van 1921 en 1959 gaven uitsluitsel over effecten van vroegere droogten. Biologische en chemische monsters van voor en na 1976 leverden inzicht in de rol van een recente extreme droogte. Dit onderzoek concentreerde zich in een drietal vennen, die blijkens de resultaten van het in Hoofdstuk 3 beschreven onderzoek verschilden in de mate van verzuring. Het vroegere milieu van deze vennen kon goed worden gekarakteriseerd met behulp van relatief veel oude planktonmonsters en oude gegevens over macrofyten en pH.

Met de hierboven beschreven historische benadering werd de ontwikkeling van de verzuring van vennen gedurende de laatste zeventig jaar beschreven. Uit paleoecologisch onderzoek bleek dat waterverzuring in Scandinavië en Groot-Brittannië tussen 1850 en 1900 is begonnen (Battarbee & Charles 1986). Gezien de aanmerkelijk hogere zure depositie in Nederland werd verwacht dat de verzuring hier eerder zou zijn begonnen. Daar chemische analyses of planktonmonsters van vennen uit de vorige eeuw ontbreken werd onderzocht of paleoecologisch onderzoek hierover informatie zou kunnen geven. Dergelijk onderzoek, waarbij restanten van organismen in onderwaterbodems (sedimenten) worden bestudeerd, is in ondiepe wateren, waar wind en bodembewonende dieren het sedimentatieproces meer dan in diepere wateren verstoren, moeilijker dan in diepe meren. Met een team biologen en een fysicus werd een methodologische studie uitgevoerd, waaruit bleek dat paleoecologisch onderzoek in vennen tot interpreteerbare resultaten kan leiden (Hoofdstuk 5). Dit leidde tot het onderzoek van Hoofdstuk 6.

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HOOFDSTUK 2

Int. Revue ges. Hydrobiol.	63	5	1978	587–607

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Man-made Changes in Some Dutch Moorland Pools, as Reflected by Historical and Recent Data about Diatoms and Macrophytes

Abstract

The diatoms of plankton samples taken between 1916 and 1929 and in 1975 from shallow pools, which were originally oligotrophic, are compared. Data about the past and present distribution of macrophytes were gathered from the literature and by field studies. Eutrophication caused by agriculture and recreation, and acidification from precipitation led to important changes in the biocenoses of the moorland pools during the last fifty years.

Contents

1. Introduction

A complex of moorland pools ("vennen", sing.: "ven") near Oisterwijk (Fig. 1) was originally oligotrophic due to its location in an area of nutrient-poor sandy soils. Until 1840, the pools were situated in vast moor and heathlands, but subsequently most of the heath and moor was reclaimed or replaced by pine forests. Most remaining oligotrophic moorland pools are now surrounded by those forests. The pools are influenced by human activities in various ways, including eutrophication from agriculture and duck farming, fishing, lowering of the groundwater table, etc.

Since the beginning of this century, the area has regularly been visited by hydrobiologists, especially by J. HEIMANS (1925, 1961, 1969), who focussed his attention on the characteristic Desmid communities. Since 1916 he observed a progressive disappearance of the most prominent and characteristic forms. In 1975, the Desmid communities were investigated again by COESEL, KWAKKESTEIN & VERSCHOOR (1978). It became evident that since 1916 these developments continued without change, i. e. the disappearance of forms continued. One group of moorland pools appeared to be eutrophied, while others seemed to be acidified.

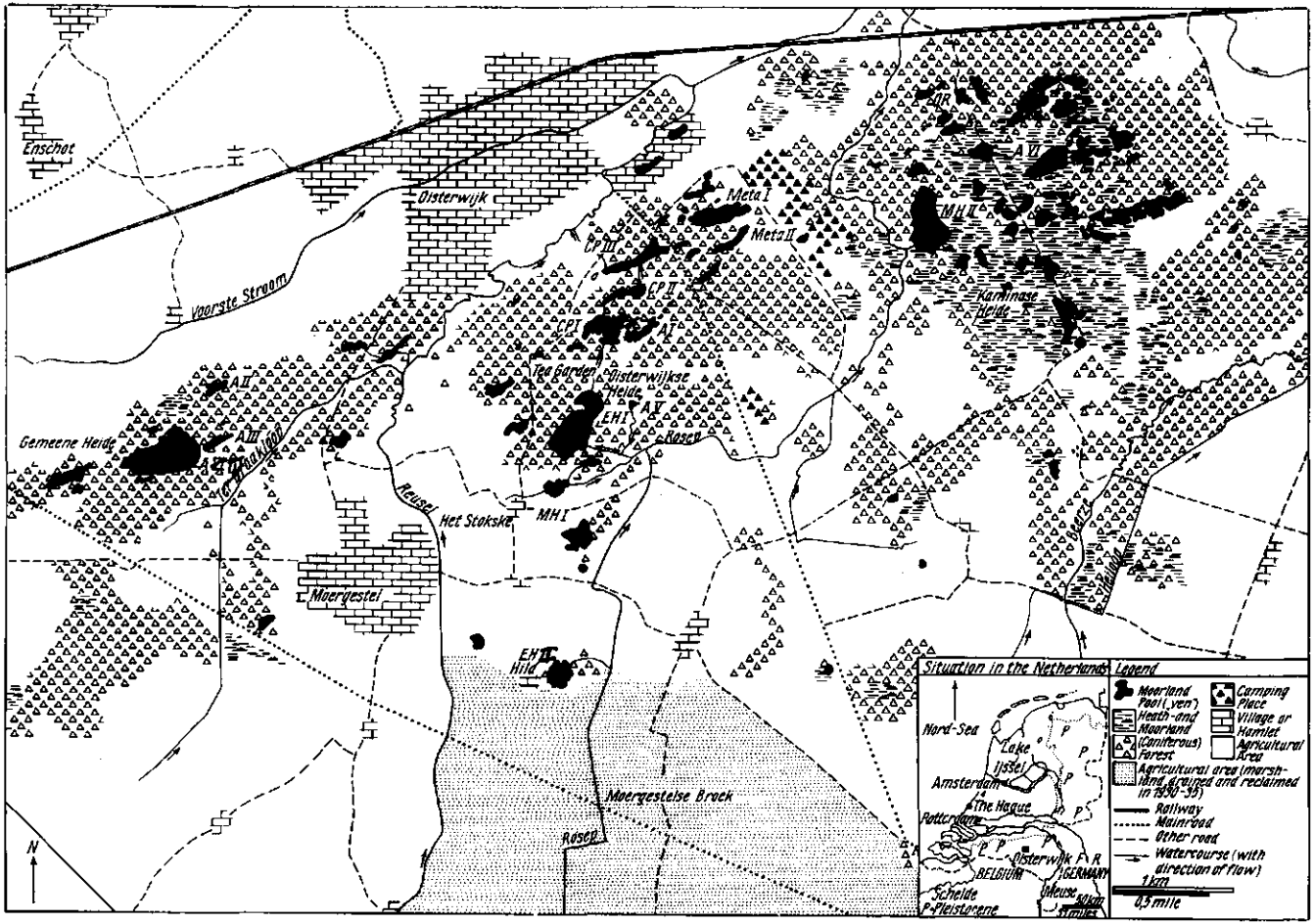

Fig. 1. Map of the study area

In order to obtain more information about the causes and the effects, both old and recent topographical and hydrographical maps were studied. From the literature, including scattered reports, relevant data about the flora were gathered. From some of the preserved samples, which were taken by HEIMANS from 1916 to 1929 and by COESEL *et al.* in 1975, diatom slides were prepared, because diatoms are good environmental indicators (see *e. g.*, VAN DAM, 1974).

2. Material and Methods

From the plankton samples (mesh width of the gauze 60µm) diatom slides were prepared by cleaning with H_2O_2 (VAN DER WERFF & HULS, 1957–1974). The cleaned frustules were embedded in Clearax and studied with a Zeiss Standard RA phase contrast microscope at a magnification of x 1250. Diatoms were identified mainly using VAN DER WERFF & HULS (1957–1974), HUSTEDT (1927–1966, 1930), PATRICK & REIMER (1966) and CLEVE-EULER (1951–1955) as references. In each slide 500 frustules were counted and subsequently the slide was scanned for species not represented in the count.

Ecological data were taken from BRADBURY (1973), CHOLNOKY (1968), FJERDINGSTAD (1965), FOGED (1964), HUSTEDT (1957), JØRGENSEN (1948), LOWE (1974), MERILÄINEN (1967), PATRICK & REIMER (1966, 1975), SCHEELE (1952), SCHOEMAN (1973), SLÁDEČEK (1973), VAN DER WERFF & HULS (1957–1974), and other publications. For each sample, the relative distribution of the 500 frustules in classes delimited along the spectra of pH, saprobity, nutrient content, salt content, etc., was calculated. This method is called 'Microalgal Spectral Analysis' (MSA) by VAN LANDINGHAM (1976).

Chemical data were borrowed mainly from routine analyses by the Dommel Water Authority (according to the methods of the Netherlands Institute for Normalization, sheet Nen 3235) and from the investigations by COESEL *et al.* (1978).

The most important sources for historical data about the moorland pools were many articles in naturalist journals (*e. g.*, THIJSSE 1915, 1916) and reports (*e. g.* VAN HEUSDEN & MEIJER, 1949; GLAS, 1957). Recent data were taken from BEIJE (1976) or collected during field excursions. Names of macrophytes are in accordance with HEUKELS & VAN OOSTSTROOM (1975), names of syntaxa are taken from WESTHOFF & DEN HELD (1969).

3. Results

3.1. *Diatom spectra and diatom flora*

There is a close correlation between the different kinds of species spectra, found in the moorland pools of the Oisterwijk area, since oligotrophy in these pools is generally associated with an acid environment. When the moorland pools become eutrophic, the pH rises. Because of this correlation, only the the pH-spectra are shown in Fig. 2. Within certain limits, it is permissible in this particular area to consider these spectra as also reflecting saprobian, trophic and halobian conditions. Changes of pH are used here as a yardstick for the trophic state of the moorland pools. In accordance with the authors mentioned previously, five classes are distinguished:

acidobiontic – occurring below pH 7 and attaining optimum development below about pH 5.5
acidophilous – occurring at about pH 7, but attaining optimum development below pH 7
circumneutral – occurring at about pH 7
alkaliphilous – optimum development above pH 7
alkalibiontic – occurring above pH 7

In the whole area 214 species and varieties were recorded; 27 had hitherto not been recorded from the Netherlands. In the samples which were taken from 1916

Table 1. Relative abundance (r. a.) of species (rows) in samples (co
+ = species present outside the count. × = species

	OR	A I		A II		A V		A VI	META I	
	1916	1919	1975	1919	1975	1929	1975	1975	1921	1975
Acidobiontic Species	24.4	31.0	63.4	30.0	96.8	67.0	79.2	43.2	72.0	32.0
Anomoeoneis serians	–	–	43.6	–	–	0.2	–	–	–	–
Eunotia exigua	5.6	2.4	11.6	6.2	86.0	1.2	60.6	39.2	12.2	16.6
Frustulia rhomboides v. *saxonica*	18.4	17.8	8.0	5.6	10.8	65.6	17.2	3.0	7.4	4.8
×*Navicula* cf. *brevissima*	–	–	–	–	–	–	0.6	0.4	42.0	0.8
×*Navicula hoefleri*	0.4	2.0	–	–	–	–	0.8	+	2.0	–
Navicula subtilissima	–	8.8	0.2	18.2	–	–	–	0.4	4.8	9.8
×*Tabellaria binalis*	–	–	–	–	–	–	–	0.2	3.6	–
Acidophilous Species	71.2	39.6	31.4	49.8	2.6	12.6	12.6	42.8	21.6	28.6
×*Achnanthes recurvata*	–	–	–	0.4	–	–	–	–	–	5.0
Eunotia alpina	–	0.6	–	–	–	1.0	–	+	–	–
×*Eunotia denticulata*	–	–	–	–	–	10.6	3.8	–	–	–
Eunotia elegans	–	–	–	21.8	1.2	–	–	–	–	3.6
Eunotia pectinalis	41.0	1.4	2.8	4.6	–	0.4	1.0	11.0	1.4	1.4
Eunotia tenella	–	–	0.8	–	–	–	–	–	7.8	1.4
Eunotia veneris	1.0	22.4	0.8	8.0	1.4	–	1.2	4.8	1.8	8.6
Frustulia rhomboides	0.4	0.2	2.2	–	–	–	–	1.4	3.2	0.2
Navicula mediocris	–	–	0.2	1.4	–	–	–	–	–	–
Peronia heribaudi	–	1.0	0.4	–	–	–	–	–	–	3.4
Pinnularia microstauron	–	–	–	0.2	–	–	0.4	–	3.0	–
×*Surirella delicatissima*	0.8	0.2	–	–	–	–	–	–	3.2	0.6
Tabellaria fenestrata	27.0	12.2	23 2	5.2	+	0.4	4.8	23.2	0.8	0.8
Tabellaria flocculosa	–	0.4	–	7.2	–	–	0.6	0.2	–	3.4
Other species	–	1.2	1.2	1.0	–	0.2	0.6	1.2	0.4	0.2
Circumneutral Species	1.4	14.4	3.8	10.8	0.2	13.2	2.4	6.0	2.2	16.6
×*Achnanthes levanderi*	–	–	–	–	–	–	–	–	–	–
Achnanthes linearis	–	–	–	0.2	–	–	–	–	–	–
Achnanthes microcephala	–	0.2	0.2	0.2	–	+	–	0.2	0.4	1.2
Cymbella cesatii	–	–	–	–	–	–	–	–	–	–
Eunotia lunaris	–	12.8	3.6	1.0	0.2	11.2	1.6	0.2	0.8	0.6
Fragilaria virescens	0.2	0.8	–	1.4	–	+	0.4	3.6	0.4	7.0
Gomphonema parvulum	–	–	–	0.8	–	–	–	0.2	–	0.2
Melosira italica	–	–	–	1.2	–	–	–	–	–	–
Navicula pupula	–	–	–	0.2	–	–	–	–	–	3.0
Navicula radiosa	–	–	–	–	–	–	–	–	–	–
Navicula radiosa var. *tenella*	–	–	–	–	–	–	–	–	–	–
Navicula rotaeana	–	–	–	–	–	–	–	–	–	–
×*Navicula tantula*	–	–	–	–	–	0.2	–	0.2	–	–
Neidium iridis	1.0	–	–	–	–	–	–	1.2	0.2	–
Nitzschia gracilis	–	0.4	–	4.6	–	–	–	–	–	–
Nitzschia palea	–	–	–	–	–	1.6	0.2	–	–	3.6
Other species	0.2	0.2	–	1.2	–	0.2	0.2	0.4	0.4	1.0
Alkaliphilous Species	1.2	12.0	1.4	8.8	0.4	4.6	5.8	7.2	2.4	18.0
Achnanthes exigua	–	–	–	–	–	–	–	–	–	0.2
Achnanthes lanceolata	–	–	–	+	0.4	+	–	–	–	1.4
Amphipleura pellucida	–	–	–	–	–	–	–	+	–	–
Amphora ovalis var. *pediculus*	–	–	0.2	–	–	–	–	–	–	–
Anomoeoneis exilis	0.4	4.0	0.2	0.6	–	+	4.0	1.8	2.2	2.8
Asterionella formosa	–	–	–	–	–	–	–	–	–	0.2

lums). Only species with r. a. $\geq 2\%$ in any sample are mentioned. hitherto not recorded from the Netherlands.

META II		CP I		CP II		CP III		MH I		MH II		EH I		EH II	
1916	1975	1919	1975	1919	1975	1922	1975	1922	1975	1922	1975	1919	1975	1916	1975
73.4	30.2	0.2	13.4	–	41.0	–	12.0	0.4	0.2	–	0.8	–	39.2	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
41.2	17.0	–	11.4	–	9.0	–	5.2	–	0.2	–	0.8	–	37.0	–	–
29.6	12.0	–	2.0		4.0	–	6.4	0.4	–	–	–	–	1.6	–	–
–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2.6	–	–	–	–	–	–	–	–	–	–	–	–	0.6	–	–
–	1.0	0.2	–	–	28.0	–	0.4	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
20.6	20.2	5.6	19.4	11.0	27.4	2.0	44.0	3.0	2.0	1.6	1.6	1.0	2.2	0.2	0.2
–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1.8	0.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	1.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	4.0	2.6	4.0	5.2	5.0	0.8	16.8	1.0	–	0.4	0.2	0.8	–	–	0.2
–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–
3.0	5.4	–	5.4	0.6	11.2	0.2	7.6	0.8	–	+	0.2	–	0.2	–	–
0.8	0.4	–	0.4	–	–	–	2.0	–	–	–	–	–	–	–	–
–	–	1.2	0.6	–	4.8	–	1.2	0.8	–	–	–	–	–	–	–
–	1.6	–	2.6	–	2.4	–	6.8	–	0.2	–	0.2	–	0.6	–	–
1.0	0.8	–	0.2	–	0.2	+	0.2	–	–	–	0.2	–	0.2	–	–
7.2	–	–	–	–	–	–	3.0	–	–	–	–	–	–	–	–
3.6	2.6	1.4	3.2	4.8	1.8	0.4	4.0	0.4	–	+	0.8	–	0.4	0.2	+
–	2.4	–	–	–	–	+	1.8	+	–	–	–	0.2	0.6	–	–
0.4	0.8	0.4	3.0	0.2	2.0	0.6	0.6	+	+	1.2	–	–	0.2	–	–
3.6	28.2	35.2	41.8	59.4	18.2	47.0	22.0	57.0	11.2	58.8	68.0	35.4	26.0	31.4	4.8
–	–	–	–	–	–	–	–	–	–	3.0	–	–	–	–	–
–	–	2.8	0.2	8.0	–	3.2	1.0	7.2	1.0	9.2	0.2	0.6	0.4	–	0.4
–	0.2	16.4	–	43.6	1.8	22.2	3.0	41.2	5.8	24.2	–	10.8	2.2	5.4	–
–	–	2.6	0.4	0.4	0.2	1.2	0.8	0.6	–	–	0.2	0.2	–	–	–
0.8	3.8	4.4	5.0	3.8	8.0	0.2	5.4	–	0.2	–	–	+	0.4	0.4	–
–	6.8	1.6	27.6	0.2	0.6	0.8	5.2	3.0	1.6	12.6	0.4	2.4	0.4	–	1.4
–	2.2	0.8	–	1.4	0.2	0.8	0.4	0.6	1.0	1.0	+	1.8	0.4	2.4	0.2
–	–	–	–	–	–	–	–	–	1.4	0.6	67.0	–	21.6	–	–
–	0.2	–	4.8	–	1.6	0.2	2.0	+	–	0.2	–	1.6	+	0.2	0.4
–	–	–	0.2	0.4	–	2.6	–	0.4	–	0.2	–	2.8	+	4.8	–
–	–	–	–	–	–	8.2	0.2	–	–	–	–	–	–	–	–
–	–	–	1.2	–	3.2	–	0.6	–	–	–	–	–	–	–	–
–	0.2	0.2	–	–	–	0.6	0.2	–	0.2	0.8	–	0.8	–	2.0	0.8
2.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	0.6	–	–	–	–	–	–	–	–	2.0	–	–	–	0.2	–
–	11.4	5.4	0.6	0.6	1.0	4.8	0.4	3.8	–	–	–	3.6	–	14.0	–
–	2.8	1.0	1.8	1.0	1.6	2.2	2.8	0.2	–	2.0	0.2	1.8	0.6	2.0	1.6
2.4	18.4	55.6	22.6	28.4	11.6	48.2	20.0	39.4	83.4	38.0	29.2	56.2	25.2	67.0	88.0
–	–	–	–	0.2	–	–	–	–	0.6	0.4	0.2	–	–	0.2	7.2
–	–	–	–	–	–	0.6	–	–	–	0.4	0.6	1.0	0.6	0.6	6.0
–	–	1.8	–	1.0	–	6.6	–	1.0	–	–	–	0.2	–	9.0	–
–	–	0.4	–	–	–	+	0.4	–	–	–	–	3.4	0.2	–	–
0.8	1.0	4.6	5.8	11.2	6.6	11.4	7.4	6.8	1.4	1.8	–	0.2	0.4	–	–
–	–	–	–	–	–	–	–	–	1.0	0.4	1.0	+	3.0	–	–

Table 1 (continued)

	OR 1916	A I 1919	A I 1975	A II 1919	A II 1975	A V 1929	A V 1975	A VI 1975	META I 1921	META I 1975
Cocconeis placentula	–	–	–	–	–	0.4	–	1.0	–	0.8
Cymbella microcephala	0.2	–	–	0.2	–	–	–	1.0	–	0.4
Fragilaria brevistriata	–	–	–	–	–	–	–	0.2	–	–
Fragilaria capucina	–	–	–	–	–	–	–	–	–	–
Fragilaria construens	–	–	0.8	2.2	–	0.4	–	0.4	–	6.0
Fragilaria pinnata	–	–	–	0.2	–	–	–	0.2	–	2.6
Melosira granulata	–	–	–	0.4	–	–	–	1.2	–	–
Navicula cari	–	8.0	–	–	–	–	–	–	–	–
Navicula cryptocephala	–	–	–	0.2	–	–	1.8	0.8	0.2	1.0
×*Navicula laterostrata*	–	–	–	–	–	–	–	–	–	–
Navicula minima	–	–	–	0.4	–	–	–	+	–	0.6
×*Navicula modica*	–	–	–	–	–	–	–	–	–	0.4
×*Navicula pseudoventralis*	–	–	–	–	–	–	–	+	–	–
Navicula schoenfeldti	–	–	–	–	–	–	–	–	–	0.4
×*Navicula seminuloides*	–	–	–	0.4	+	–	–	–	–	–
Navicula seminulum	–	–	–	–	–	–	–	–	–	0.4
Navicula viridula	–	–	–	–	–	–	–	–	–	–
Navicula vitabunda	–	–	–	–	–	–	–	–	–	–
Nitzschia cf. *confinis*	–	–	–	–	–	–	–	–	–	–
Nitzschia fonticola	–	–	–	–	–	0.2	–	0.2	–	–
Nitzschia linearis	–	–	–	–	–	–	–	–	–	–
Synedra acus	–	–	–	–	–	–	–	–	–	–
Synedra tabulata	–	–	0.2	–	–	1.0	–	–	–	0.2
Synedra tenera	–	–	–	–	–	–	–	–	–	–
Other species	0.6	–	–	4.2	–	2.6	–	0.4	–	0.6
Alkalibiontic Species	–	–	–	–	–	1.4	–	–	–	1.0
Achnanthes conspicua	–	–	–	–	–	–	–	–	–	0.2
Stephanodiscus astraea	–	–	–	–	–	–	–	–	–	–
Stephanodiscus dubius	–	–	–	–	–	–	–	–	–	–
Other species	–	–	–	–	–	1.4	–	–	–	0.8
Unidentified species	1.8	3.0	–	0.6	–	1.2	–	0.8	1.8	3.8

to 1929, 187 taxa were found; in the samples from 1975, 164 taxa were present. Species with a relative abundance $\geq 2\%$ are listed in Table 1 according to their pH-class.

3.2 *The original state of the moorland pools*

As may be expected in an area with oligotrophic soils, and as shown by older records, the original biocenoses in the moorland lakes are characteristic of a nutrient-poor environment.

In the shallowest pools (about 0.5 to 1.5 m deep), the organic materials accumulate on the bottom and *Sphagnum* spp. grow luxuriantly. *Juncus bulbosus* f. *fluitans* is the only submerged seed-plant. Belts of *Carex rostrata* and *Eriophorum angustifolium* surround these moorland pools. *Drosera* spp. are found on hummocks of peat-moss (Table 2, vegetation type 1).

In larger and deeper pools (2–3 m), situated in heathlands, the sandy bottom is kept bare by the action of wind and waves. The Isoeto-Lobelietum association was widely distributed in these pools (vegetation type 2).

META II		CP I		CP II		CP III		MH I		MH II		EH I		EH II	
1916	1975	1919	1975	1919	1975	1922	1975	1922	1975	1922	1975	1919	1975	1916	1975
–	5.2	–	–	1.2	0.2	0.6	–	1.2	0.6	0.2	+	8.8	1.2	17.6	0.8
–	–	2.2	2.2	1.0	0.2	8.2	0.6	6.2	0.2	10.2	–	3.2	0.2	–	–
–	0.2	0.6	1.2	–	–	+	0.2	1.0	0.4	0.6	0.8	2.2	+	0.2	2.4
–	–	–	–	–	–	–	–	–	0.2	3.6	–	1.6	+	1.8	–
–	7.6	14.0	7.8	2.2	3.2	4.4	3.8	5.6	4.4	5.2	20.6	14.0	1.0	1.8	22.0
–	1.6	11.8	0.8	0.8	0.4	4.6	0.2	1.2	5.6	1.8	1.2	6.4	0.6	3.4	19.2
–	0.6	–	–	–	–	–	–	–	32.8	–	+	–	11.4	–	0.6
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1.4	0.4	1.8	0.4	2.2	–	1.2	0.4	0.6	0.8	0.6	+	4.0	0.6	15.4	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.0
–	–	2.8	0.6	0.2	0.2	1.4	0.2	0.2	0.8	3.0	0.2	1.4	0.6	0.8	1.4
–	–	8.0	–	0.2	0.2	+	2.4	–	1.2	0.6	0.2	1.2	–	0.2	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14.4
–	–	–	–	–	–	–	–	–	1.2	–	1.2	–	0.2	1.0	7.6
–	–	–	–	–	–	–	–	–	–	3.2	–	–	–	–	–
–	–	0.4	1.0	0.8	–	1.0	0.6	1.8	1.8	1.2	–	0.8	0.2	1.2	2.0
–	–	2.4	0.4	0.2	–	–	0.2	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	2.8	1.6	–	–	–	–	–	2.0
–	–	–	–	–	–	–	–	–	–	–	–	–	–	9.0	–
0.2	–	0.2	0.2	0.4	–	1.0	–	7.4	0.8	1.2	–	2.6	0.2	–	–
–	–	–	–	–	–	–	–	–	–	0.4	–	–	–	–	–
–	0.2	–	–	–	–	0.2	–	–	19.0	0.4	0.2	–	–	–	–
–	–	–	–	–	–	0.2	0.4	–	7.0	–	–	–	–	–	–
–	–	2.0	–	3.4	–	1.6	–	0.6	–	0.6	–	0.4	–	0.6	–
–	2.6	2.6	2.2	3.4	0.6	5.2	3.2	3.0	2.0	2.2	3.0	4.8	4.8	4.2	0.4
–	3.0	0.6	0.8	–	–	2.6	–	0.2	3.2	0.2	0.2	5.6	7.4	1.4	5.0
–	–	0.6	0.4	–	–	1.2	–	0.2	0.4	+	–	2.2	0.6	–	4.8
–	0.4	–	–	–	–	–	–	–	2.4	–	–	–	1.0	–	0.2
–	–	–	0.4	–	–	–	–	–	–	–	–	–	5.2	–	–
–	2.6	–	–	–	–	1.4	–	–	0.4	0.2	0.2	3.4	0.6	1.4	–
–	–	2.8	2.0	1.2	1.8	0.2	2.0	–	–	0.4	0.2	1.8	–	–	2.0

At the transition of nutrient-poor cover-sands and loamy depositions of the rivulets there was an oligo-mesotrophic environment. These conditions were optimal for many species of the Eleocharetum multicaulis and the Potamion graminei (vegetation type 3).

The original chemical composition of the water and the diatom associations of the pools with the above-mentioned vegetation types cannot be adequately described because the material is scarce. In all three types species of acid, oligotrophic environments, *Frustulia*, *Eunotia*, *Pinnularia* etc. dominated as can be seen in the analyses of metatrophic moorland pools Meta I (1921), Meta II (1916) and OR (1916) (Table 1, Fig. 3b, c). In Table 3 the chemical conditions in those moorland lakes are listed, which are supposed to be undisturbed. The data are derived from measurements in the least disturbed pools in 1975–1976 and from some scarce analyses dating from 1920–1926.

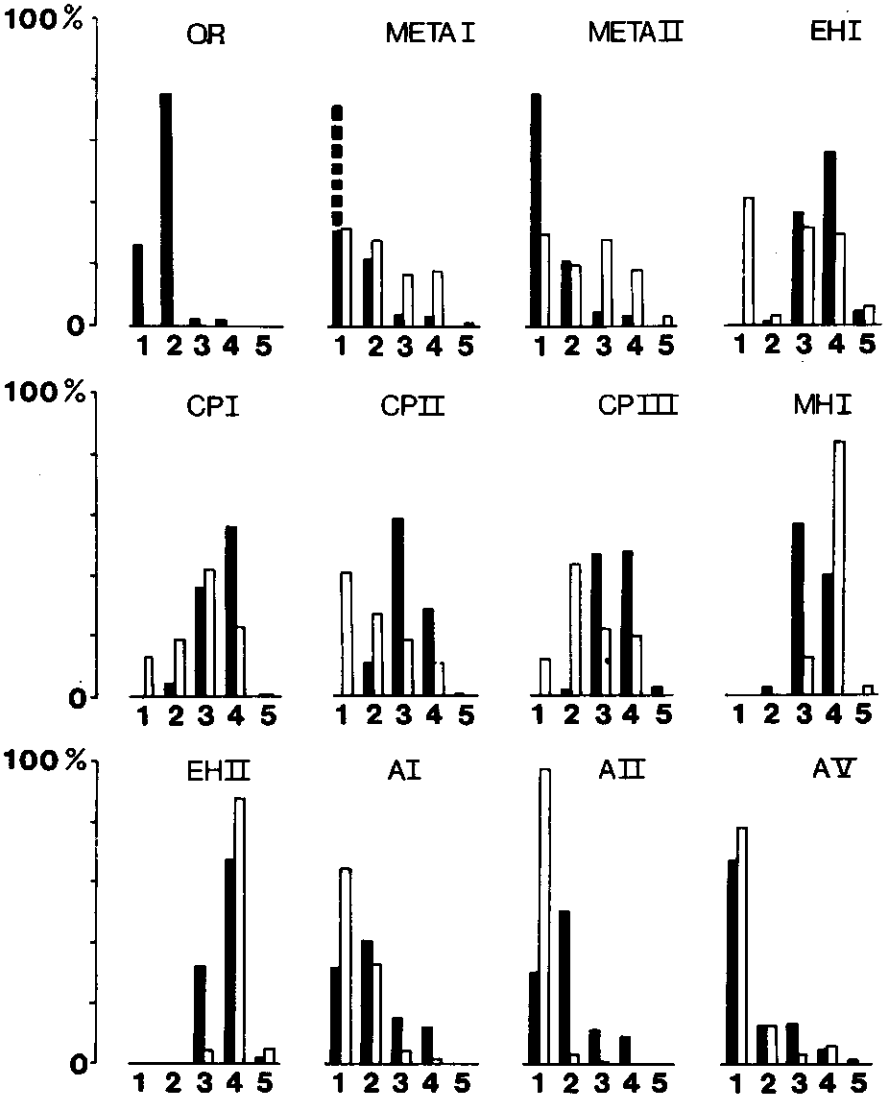

Fig. 2. Histograms of pH spectra. Ordinate: relative abundance of pH-groups. Abscissa: pH-groups (1 = acidobiontic, 2 = acidophilous, 3 = circumneutral, 4 = alkaliphilous, 5 = alkalibiontic). Black bars 1916–1929, white bars 1975. The broken part of the first bar of META I represents the relative abundance of *Navicula* cf. *brevissima*, which may be either acidobiontic or acidophilous.

Table 2. Chemical composition of the water in different types of moorland pools

property	unit	oligotrophic oligo-dystrophic oligo-mesotrophic	eutrophic hypertrophic
pH		3.1–5.4	6.5–9.2
Conductivity (25 °C)	μS/cm	44–140	85–285
Idem, corrected for pH	μS/cm	<120	85–285
Oxygen saturation	%	68–125	46–168
BOD_2^{25}	mg O_2/l	0.4–7.1	0.8–16
Coli-Eijkman	MPN	≦4,9	≦17
NH_4^+-N	mg/l	0.1–2.2	0.1–4.2
NO_2^-N	mg/l	≦0.05	≦0.05
NO_3^--N	mg/l	≦0.2	≦0.6
PO_4^{3-}-P (ortho)	mg/l	≦0.02	≦0.2
PO_4^{3-}-P (total)	mg/l	≦0.1	≦1.0
Cl^-	mg/l	6–14	20–35
SO_4^{2-}	mg/l	5–10	20
Na^+	mg/l	3–8	10–14
K^+	mg/l	1–2	6–8
Ca^{2+}	mg/l	1–5	14–27
Mg^{2+}	mg/l	1–2	3–5
Total hardness	°D	0.4–1.0	1.3–7.0
Alkality	meq/l	<0.1	0.6–1.5
SiO_2	mg/l	<0.6	0.3–9.7
Fe	mg/l	≦0.2	≦0.9
Colour	mg Pt/l	2–8	15–69

Table 3. Vegetation types. Species between brackets characterize more than one group. Species with an apostrophe are trivial and may be found both in well-developed and in degenerated specimens of the type

Vegetation type	Related syntaxa	Characteristic species
1. oligo-dystraphentic	Rhynchosporion alba, Oxycocco-Sphagnetea	*Andromeda polyfolia, Carex lasiocarpa, C. rostrata', Drepanocladus fluitans', Drosera intermedia, D. rotundifolia, (Eleocharis multicaulis), Erica tetralix', Eriophorum angustifolium', Juncus bulbosus', (Menyanthes trifoliata), Molinia caerulea', Myrica gale', Narthecium ossifragum, (Nymphaea alba'), Oxycoccus palustris, (Potentilla palustris), Sphagnum crassicladum', Sphagnum* div. spec., *(Utricularia minor). Hydrocotyle vulgaris* and *Juncus effusus* may indicate irregular changes of the water table, guanotrophy, or beginning eutrophication by agriculture.
2. oligotraphentic	Isoeto-Lobelietum (Littorellion p. p.)	*Isoetes lacustris, (Littorella uniflora), Lobelia dortmanna*
3. oligo-mesotraphentic	Potamion graminei Eleocharetum multicaulis (Littorellion p. p.)	*Apium inundatum, Deschampsia setacea, Echinodorus repens, (Eleocharis multicaulis), Hypericum elodes', (Littorella uniflora), Luronium natans, Myriophyllum alterniflorum, (Nymphaea alba), Pilularia globulifera, Potamogeton gramineus, (P. natans'), P. polygonifolius, Ranunculus flammula', R. ololeucos, Scirpus fluitans, Sparganium angustifolium, S. minimum, Utricularia intermedia, (U. minor), U. ochroleuca, Veronica scutellata*

Table 3 (continuation)

Vegetation type	Related syntaxa	Characteristic species
4. eutraphentic	Magnopotametalia Hydrocharition Phragmition Magnocaricion	*Alisma plantago-aquatica', Carex pseudocyperus, Cicuta virosa, Elodea canadensis, Equisetum fluviatile, Hydrocharis morsus-ranae, Mentha aquatica', (Menyanthes trifoliata), Nuphar lutea', (Nymphaea alba), Nymphoides peltata, Phragmites australis, Potamogeton lucens, (P. natans), P. praelongus, (Potentilla palustris), Rumex hydrolapathum', Ranunculus lingua, Stratiotes aloides, Typha* spp., *Utricularia vulgaris, Scirpus lacustris'. (Rorippa amphibia)* may indicate irregular changes of the water table.
5. saprobic	Bidention, Agropyro Rumicion crispi and others	*Glyceria maxima, Epilobium hirsutum, Lemna minor, Lycopus europaeus, Oenanthe aquatica, (Rorippa amphibia), Polygonum hydropiper, Spirodela polyrhiza.*

Fig. 3. The most abundant or most typical diatom species from some samples with their relative abundances. a) CP I, b) META I, c) A I.

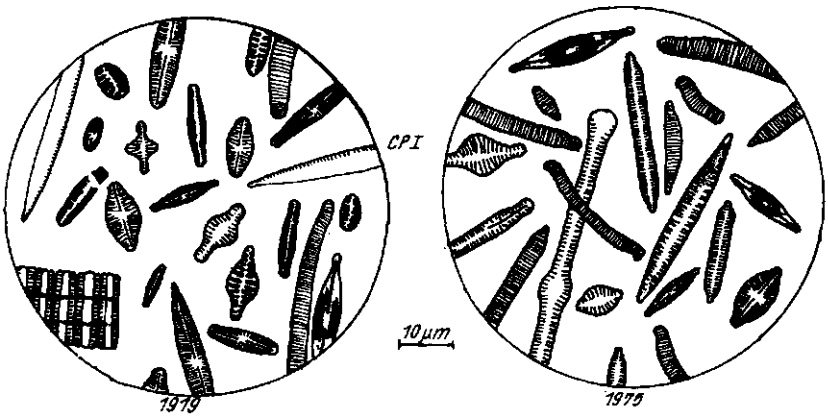

Fig. 3a

Achnanthes microcephala	16%	*Fragilaria virescens*	28%
Fragilaria construens	12	*Eunotia exigua*	11
Fragilaria pinnata	12	*Eunotia lunaris*	5
Navicula modica	8	*Eunotia veneris*	5
Anomoeoneis exilis	5	*Navicula pupula* v. *mutata*	5
Nitzschia palea	5	*Anomoeoneis exilis*	6
Eunotia lunaris	4	*Fragilaria construens*	4
Achnanthes linearis	3	*Fragilaria constr.* v. *venter*	3
Cymbella cesati	3	*Tabellaria fenestrata*	3
Navicula minima	3	*Eunotia pectinalis* v. *minor*	4
Eunotia pectinalis v. *minor*	3	*Surirella delicatissima*	2
Cymbella microcephala	2	*Peronia heribaudi*	2
		Cymbella microcephala	2

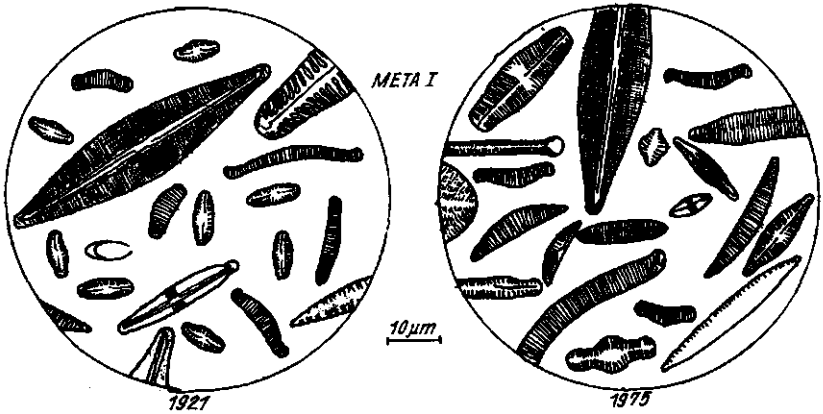

Fig. 3b

Navicula cf. *brevissima*	42%	*Eunotia exigua*	17%
Eunotia exigua	12	*Eunotia veneris*	9
Eunotia tenella	8	*Fragilaria virescens*	7
Frustulia rhomboides var. *saxonica*	7	*Achnanthes recurvata*	5
Navicula subtilissima	5	*Frustulia rhomboides* var. *saxonica*	5
Tabellaria binalis (septum)	4	*Fragilaria construens* v. *venter*	4
Pinnularia microstauron	3	*Nitzschia palea*	4
Surirella delicatissima	3	*Eunotia elegans*	4
Eunotia veneris	2	*Peronia heribaudi*	3
		Tabellaria flocculosa	3
		Navicula pupula	3
		Amphora veneta	.6
		Asterionella formosa	.2
		Cocconeis placentula	.8

3.3 *Man-made changes*

Three important processes take place in the moorland pools: eutrophication from agriculture (and birds), eutrophication through swimming and fishing activities, and acidification by precipitation. To facilitate the orientation, the following letter combinations are used to designate the moorland pools as follows:

EH – moorland pools which were already eutrophic about 1920 and are now hypertrophic (frequent blooms of blue-green algae)
MH – moorland pools which were mesotrophic about 1920 and are now hypertrophic
META – moorland pools which were oligotrophic or oligo-dystrophic about 1920 and are now metatrophic, *i. e.*, both oligotraphentic and eutraphentic organisms are present
CP – central pools which were mesotrophic about 1920 and have since become acidified
A – moorland pools which were oligotrophic or oligo-dystrophic about 1920 and have since become acidified

The abbreviations are followed by roman numerals (Fig. 1).

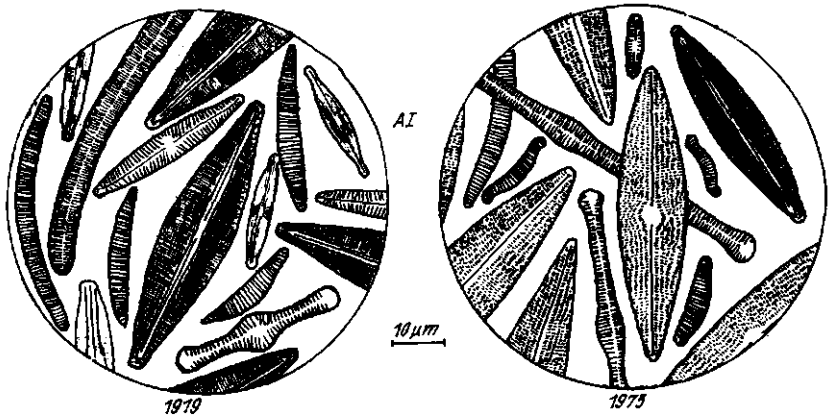

Fig. 3c

Eunotia veneris	22%	*Anomoeoneis serians*	44%
Frustulia rhomboides var. *saxonica*	18	*Tabellaria fenestrata*	23
Tabellaria fenestrata	12	*Eunotia exigua*	12
Eunotia lunaris	12	*Frustulia rhomboides* var. *saxonica*	8
Navicula subtilissima	9	*Eunotia lunaris*	4
Navicula cari	8	*Eunotia pectinalis* var. *minor*	3
Anomoeoneis exilis	6	*Navicula mediocris*	.2
Navicula hoefleri	2		

3.3.1 Eutrophication by agriculture

Moorland pool EH I was already connected with the mesotrophic rivulet Rosep (Fig. 4a, b) before 1835, when the first reliable and detailed maps were produced. Moreover, EH I received the drainage water of the fields around the hamlet "Het Stokske". Therefore, this pool was already eutrophic by the beginning of this century, as can be concluded from the fragmentary data about plankton and vegetation (type 4). The diatom association in 1919 also indicates alkaline eutrophic conditions (Fig. 2). This situation may have already existed for a long time, because the local population must have used fish from the pool as a source of protein. A rather similar situation was found in MH I, which was also connected with the Rosep.

About 1840 CP I was connected by a ditch with EH I. CP I, CP II and CP III became serially connected in c. 1870. CP III drained into the rivulet Reusel (Fig. 1). In this way EH I discharged eutrophic water via the central pools into the Reusel.

Consequently, the original stands of vegetation on the CP's (types 1 and 2) gradually disappeared, most rapidly in CP I and most slowly in CP III. In the main current, type 4 vegetation developed very well (Fig. 4c). The water soldier (*Stratiotes aloides*) was very abundant, owing to the slight manuring by the influx of draining water. The water soldier and other plants were dredged every autumn by the local farmers to fertilize their fields. Nutrients were removed from the water by this

Fig. 4. *a*) The rivulet Rosep in the Moergestelse Broek

b) The rivulet Rosep in the nature-reserve (*a*, *b* JOOP VAN OSCH)

c) Typical aspect of the central pools in 1923 (JAN STRYBOS)

d) Typical aspect of the central pools in 1977 (PETER COESEL)

e) The oligo-dystrophic Lammerven (A V) (JOOP VAN OSCH)

action, which is the only way to assure the continued existence of *Stratiotes*-fields (G. VAN WIRDUM, pers. comm.).

Between the eutrophic main current and more remote locations which remained oligotrophic due to percolation of nutrient-poor ground water, mesotrophic conditions were produced. This became an environment well suited for type 3 vegetation. At some places mesotraphentic quivering bogs were found, with a Scorpidio-Caricetum diandrae association (*Scorpidium scorpioides*, *Carex lasiocarpa*, *Eriophorum gracile*).

The diatom communities of the CP's in 1919–1922 indicate neutral to alkaline conditions (Figs. 2, 3a), but acidophilous species occurred as well, as is expected in accordance with the local vegetation types. Several colorimetric pH-measurements in 1925–1929 gave values of pH 7–8.

In 1916, a tea-garden was built near the connecting ditch between EH I and CP I. The sewage water was discharged into the ditch, and consequently a saprobic type of vegetation developed in part of CP I (type 5 vegetation) (VAN DIJK *et al.*, 1960). For this reason, the CP's were cleaned in 1950–1951 (VAN DER WERFF, 1955). CP I and II were completely drained by pumps and the stands of vegetation and the bottom sludge were removed. After this operation the pools filled spontaneously with upwelling ground water. The discharge of sewage was discontinued, and the connection with EH I was severed. At that time a process of acidification began in the central pools.

EH I has become hypertrophic since that time. Blue-greens are frequently observed, and the stands of vegetation (type 4) degenerated, with submerged water plants completely disappearing. The cause is the excessive inflow of nutrients from drainage

Fig. 4f) The metatrophic Groot Aderven (META II) (JOOP VAN OSCH)

of the arable land near "Het Stokske" (Fig. 1) and the Rosep. Before the reclamation in the "thirties" of the area where this rivulet originates, the water was mesotrophic to eutrophic. After reclamation, the pastures were amply fertilized and intensive live-stock production developed especially in the last decade. Consequently the rivulet became polluted by drainage and sewage water. The pH-spectrum of EH I (Fig. 2) shows a bimodal curve. The acidobiontic maximum is caused by *Eunotia exigua*. The explanation of the present abundance of this species is obscure. All other species are typical of neutral to alkaline eutrophic environments.

Similar processes occurred in EH II, which was also connected with the rivulet Rosep since prior to 1900 and likewise received drainage water from a neighbouring hamlet. MH I had a connection with the Rosep about 1900. The stands of vegetation belonged to type 2 and partly to type 3 owing to the slight eutrophication. The diatom association (Table 1) indicated neutral to alkaline conditions. Since then, MH I became a blue green coloured pool from the influx of eutrophic drainage water and from guanotrophy (rearing of ducks). MH II was hypertrophied not only from an influx of

Rosep water, but also by sport fishing (foddering and fertilizing). In Table 3 the chemical conditions of the MH's and EH's in 1975–1976 are presented. The effects of enrichment with nutrients are obvious.

3.3.2 Swimming and sport-fishing

META I was famous for its vegetation of *Lobelia dortmanna* and *Isoetes lacustris* (type 2), and remained so until late into this century. This pool is traditionally used as a swimming pool. The numbers of visitors were very limited in earlier days, but now 20,000 or more people bathe here annually. *Lobelia* and *Isoetes* have now disappeared. In 1921 the diatoms (Figs. 2, 3b) indicated acid conditions. *Tabellaria binalis*, typical of *Lobelia*-lakes in Northern Europe, occurred here (Table 1). Since then this species has disappeared from META I. The pH-spectrum indicates metatrophic conditions, so that oligotraphentic and eutraphentic species are present without a special optimum in the mesotrophic area. The actual measurements of the pH give values between 3.4 and 7.0.

Rather similar developments took place in META II (Fig. 4f). This pool has been used as a fish pond since 1932. To create suitable conditions for the fish-stock, the "ven" was regularly limed and fertilized, and the fishes were fed. In earlier times the vegetation contained elements of the types 1, 2 and 3. At present, species of the types 1, 4 (degenerated) and 5 are present. The diatoms (Fig. 2) also indicate metatrophic conditions.

3.3.3 Acidification

After cleaning, the central pools acidified rapidly (VAN DER WERFF, 1955; VAN DIJK et al., 1960). This can also be deduced from the pH-spectra (Fig. 2). The type 4 and 5 vegetation greatly diminished and disappeared rapidly. The type 1 and 3 vegetation developed luxuriantly in the "fifties", but now type 3 has degenerated with only *Hypericum elodes* remaining rather abundant.

The acidification is not only visible in these three moorland pools but also in isolated pools such as A I, A II and, to a lesser extent, A V (Figs. 2, 3c, 4e). The vegetation stands of these pools belong mainly to type 1, but in A II, elements of type 2 were also to be found in earlier days. A decrease of type 2 is also known from other isolated moorland pools in the area, such as A III, A IV, and A VI. Unfortunately, no detailed chemical analyses of these pools are known to have been made in the twenties, but HEIMANS (pers. comm.) never measured pH < 4 by colorimetric field methods. In 1975–1976 considerably lower values were measured frequently, e. g., pH 3.1 in A IV. Only in A II, a time series can be reconstructed from such measurements: 1925: pH 6–6.3; 1947: pH 5.2; 1975: pH 3.8.

The most probable reason for the rapid decrease of the pH in the moorland pools is the acidification of the precipitation, which has been observed since the "fifties" all over Western Europe. From the data supplied by VERMEULEN (1977) it can be calculated that the natural deposition of SO_2 in a moorland pool with an area of 15 ha (like A IV) should be less than about 0.3 ton/year. The actual deposition is 0.8–1.5 tons/year.

Comparative hydrobiological changes by an acidification of precipitation are reported by GRAHN (1976) and HENDREY *et al.* (1976), who observed a severe decrease of our type 2 vegetation in Swedish lakes caused by a decline of pH from about 6 to about 4 in the last thirty years. ALMER *et al.* (1974) deduced a lowering of the pH from a shift in the species composition of benthic diatom communities in a Swedish lake.

4. Discussion

The natural history of the moorland pools near Oisterwijk illustrates the processes that have influenced the Dutch environment in general. Until the end of the 19th century, man (i. e., the farmer) enhanced the diversity of the landscape. The largest part of the Pleistocene area in The Netherlands (bordered by dotted lines in the inset of Fig. 1) was still oligotrophic. Relatively nutrient-rich areas, such as the lower reaches of the brook-valleys or the immediate surroundings of human settlements, were only small nuclei in the predominantly seminatural landscape.

By small-scaled human activities, the differentiation of the environment increased. Pre-existing trophic gradients (gradual transitions) were enhanced and new ones were created, as in the central series of moorland pools in our area. By creating a complex trophic gradient in a prevailingly oligotrophic environment, suitable conditions for mesotraphentic organisms were produced, which were previously almost non-existent. In this way, external forces promoted the diversity within and among the moorland pools.

In our century, however, technology advanced and it became possible to reclaim and drain areas which had earlier been unsuitable for cultivation because of swampiness and/or lack of sufficient nutrients. Artificial fertilizers became available and are used in large quantities. Intensive live-stock farming produces a surplus of slurry, which is spread over the fields. Consequently, oligotrophic areas now comprise only small islands in vast eutrophic areas, in contrast with the original situation. An inversion of the trophic pattern of the landscape has taken place. Oligotrophy no longer dominates over eutrophy and gradients are difficult to maintain (VAN LEEUWEN, 1966; SCHROEVERS, 1966a, b).

When the catchment area in the upper reaches of the rivulet Rosep was reclaimed, the water in the brooklet eutrophied in such a way that EH I became hypertrophic. The connection with CP I was cut off to prevent hypertrophy of the three central pools. As a consequence, the conditions of existence for the trophic gradient were removed and the oligo-mesotraphentic macrophytes disappeared. They were not replaced by the oligotraphentic macrophytes of type 2, which inhabited the pools before 1840.

In some isolated pools, acid precipitation acidified the water. Here the oligotraphentic type 2 is replaced by elements of the oligo-dystraphentic type 1. The environment of type 1 has also changed, however, as observed in the very dry summer of 1976. On the dry shores, seedlings of the Bidention and of related species were frequently observed (*Polygonum hydropiper*, *Lycopus europaeus*, *Eupatorium cannabinum*, etc.). In former times instead of these species, elements of the Nanocyperion, especially of the Cicendietum filiformis, became abundant in dry years (*Cicendia filiformis*, *Juncus mutabilis*, *Pilularia globulifera* etc.). We may conclude from these facts that the moorland pools are acidified by the precipitation, but that this does not necessarily mean an oligotrophication or a decrease of nutrients. Owing to the appreciable deposition of sulphates, nitrates and other ions, more nutrients may become available for the plants.

Many of the other moorland pools are eutrophied through human activities such as swimming, fishing and agriculture. The original biocenoses disappear in such lakes. The types 1 and 2 vegetation are replaced by type 5 or by impoverished forms of type 4 (without *Stratiotes aloides*, etc.).

The developments in the composition of the diatom communities also indicate that only two types of communities will survive in future, viz., the type of extremely acid environment (characterized by *Eunotia exigua* and *Frustulia rhomboides* var.

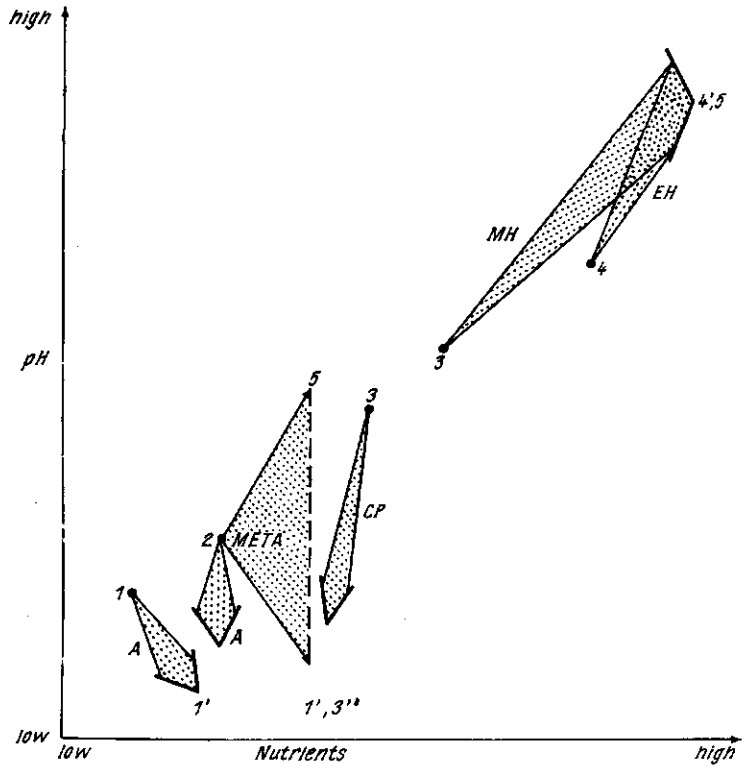

Fig. 5. Diagrammatic representation of the impact of eutrophication and acidification on different types of moorland pools (designated by letters). Numbers indicate vegetation types; an apostrophe indicates degeneration of the type. The base of an arrow represents the situation by about 1920, the head that of 1975.

saxonica) and the eutrophic-saprobic one (characterized by *Asterionella formosa*, *Melosira granulata*, *Synedra acus*, *Nitzschia palea*, etc.). The mesotraphentic species will disappear or greatly diminish. The processes are summarized in Fig. 5.

5. Summary and Conclusions

1. The spectral analysis of diatom communities is a suitable method for tracing ecological differences within and among moorland pools.

2. A comparison of historical with recent data concerning the macrophytes may give reliable information about anthropogenic changes in the environment.

3. In nearly all moorland pools near Oisterwijk the biocenoses have seriously deteriorated as the result of human activities in the last hundred years. Agriculture, recreation and acidification of precipitation are especially important factors. By the inversion of the trophic pattern of the landscape, trophic gradients cannot be main-

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tained and the biological differentiation within and among the pools declines considerably.

4. Most probably, only two types of moorland pools will ultimately survive viz., the hypertrophic type (enriched by run-off and drainage water, fishing etc.) and the extremely acid type (acid precipitation). The processes are summarized in Fig. 5.

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Impact of acidification on diatoms and chemistry of Dutch moorland pools

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Keywords: acidification, diatoms, dissimilarity, diversity, moorland pools, principal component analysis

Abstract

Old (ca 1920) and recent (1978) diatom assemblages from sixteen pristine moorland pools are compared by analysis of pH-spectra, diversity (Hill's index), (dis)similarity (number of species in common, Dyer dissimilarity) and principal component analysis. The pH-spectra of clear water pools indicate that the formerly wide range of pH (4–6) is very narrow now (3.7–4.6). No significant change of pH (ca 4.5) is observed in brown water moorland pools. Diversity significantly declines in clear water pools and has a tendency to rise in brown water pools. The number of species in common does not change. The Dyer dissimilarity significantly decreases in clear water lakes, no change is found in brown water lakes. The first principal component (PC 1) explains 61% of total variance between samples and is nearly completely determined by *Eunotia exigua*. PC 1 has a strong positive correlation with both the absolute and relative sulfate concentration and other factors related to acidification (Ca^{2+}, Al^{3+}, Mg^{2+}, electrical conductivity). PC1 has a negative correlation with factors characterizing humic acid waters ($KMnO_4$-consumption, Fe, $(Na^+ + K^+)/(Ca^{2+} + Mg^{2+})$ etc.). Old samples have low scores on PC 1. Recent samples from clear waters have high scores on PC 1. The original variation, caused by regional factors, is replaced by a sulfate controled variation. The factors which are responsible for the recent differences in sulfate concentrations between pools are discussed (sulfate reduction, accumulation by dry deposition in adjacent pine forests and drought). Some observations contribute to the opinion that acidification may be considered as eutrophication and not as oligotrophication.

1. Introduction

The growing use of fossil fuels has caused an increase of atmospheric sulfur in the last decennia. The deleterious effects of acid rain upon aquatic ecosystems have been studied in Scandinavia and North America (Braekke 1976; Almer *et al.* 1978). The extinction of fish populations is very obvious, but also other components of the ecosystem, *viz.* the species composition of plankton and periphyton changes thoroughly by acidification.

The Netherlands are in the very centre of the acid rain area of north-western Europe (Granat 1978). World's lowest annual mean pH yet recorded is 3.8 in 1967 at De Bilt (Fig. 1). The present pH of precipitation is about 4.3 (Anonymous 1979).

In spite of this severe pollution no investigations focussed on this problem have been carried out in the Netherlands up to now, although Coesel *et al.* (1978) and Van Dam & Kooyman-van Blokland (1978) present strong evidence for the adverse effects on desmids and diatoms in moorland pools (Dutch: ven; German: Heidetümpel). These waters are in a geologic environment that is highly resistant to chemical weathering and have relatively low concentrations of major ions and hence a low buffer capacity. Such waters are extremely vulnerable to inputs of acid precipitation (Wright & Gjessing 1976).

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Fig. 1. Location of the study areas. x = rainwater gauge (Anonymous 1979).

Diatoms are widely used as pH-indicators in actuo- and palaeolimnology since the conception of the pH-classification scheme of freshwater diatoms by Hustedt (1939). Miller (1973) and Berge (1979) used the diatom assemblages in cores of Scandinavian lake sediments as a record of past pH-conditions to assess the impact of acid precipitation. Berge (1976) compared diatom samples from 1949 and 1975 to establish a decrease of pH in some south Norwegian streams and ascribed this shift to the acidification of precipitation.

Many moorland pools are shallow and poor in sediments. Therefore we used old samples to estimate the past environmental conditions. A large number of algal samples in moorland pools have been collected between 1916 and 1955 for studies on desmids (see *e.g.* Heimans 1969). In 1978 new samples were taken at the same sites.

According to the theories of Thienemann (1920), Franz (1953), Van Leeuwen (1966), Margalef (1975) and May (1975) complex and delicately balanced ecosystems are confined to a predictable environment (stable conditions) with a low input of energy and matter. Complex natural ecosystems (with a high diversity) are fragile, *i.e.* very sensitive to perturbation. Perturbation means a relatively unpredictable environment, with a high input of energy and matter. These unstable conditions only permit structurally simple, robust ecosystems (with a low diversity) to exist.

The pH of unpolluted rainwater, in equilibrium with CO_2 in the atmosphere is 5.6–5.7. The present pH of many moorland pools is in between 3.5 and 4.0. This is a difference of about 200 μeql^{-1} H^+. With this increase in hydrogen ion concentration all original pH-values of the moorland pools between about 4 and 6 will be concentrated in the narrow range between 3.5 and 4.0. So, similarity of the environment in the moorland pools will increase by acidification.

It may be expected therefore that acidification causes a decrease of diversity and dissimilarity of the diatom assemblages in moorland pools. We will test these hypotheses. Besides, the acidification is shown by comparison of pH-spectra of old and recent diatom samples. Multivariate analysis of data gives insight to changes in species composition, diversity, dissimilarity and their relationships with water chemistry.

Also other processes than pollution of rain water may be responsible for the acidification of moorland pools, *e.g.* the severe drought of 1976 and the reafforestation of the catchments. Their significance will be discussed.

2. Study sites

Moorland pools are shallow (depth less than ca 3 m) soft water lakes with no visible in- and efflux. They are part of the heath (podzol) landscape with poorly buffered sandy soils. The surface area of the sixteen pools we studied (Fig. 1; Table 1) varies from about 0.1 to 15 ha.

Eight pools are situated in the province of North-Brabant, near Oisterwijk (B), two in the Veluwe area (V), and six in the province of Drenthe (D).

The bottom of most pools in the B- and V-districts is sandy and often covered with a thin layer of detritus and peat. No detailed knowledge about the hydrology of most pools is available. V1 (Fig. 2) and V2 are situated some tens of meters above the aquifer. Their watershed is hardly larger than their surface and sealed by an impermeable iron-pan

Table 1. Physico-geographical data.

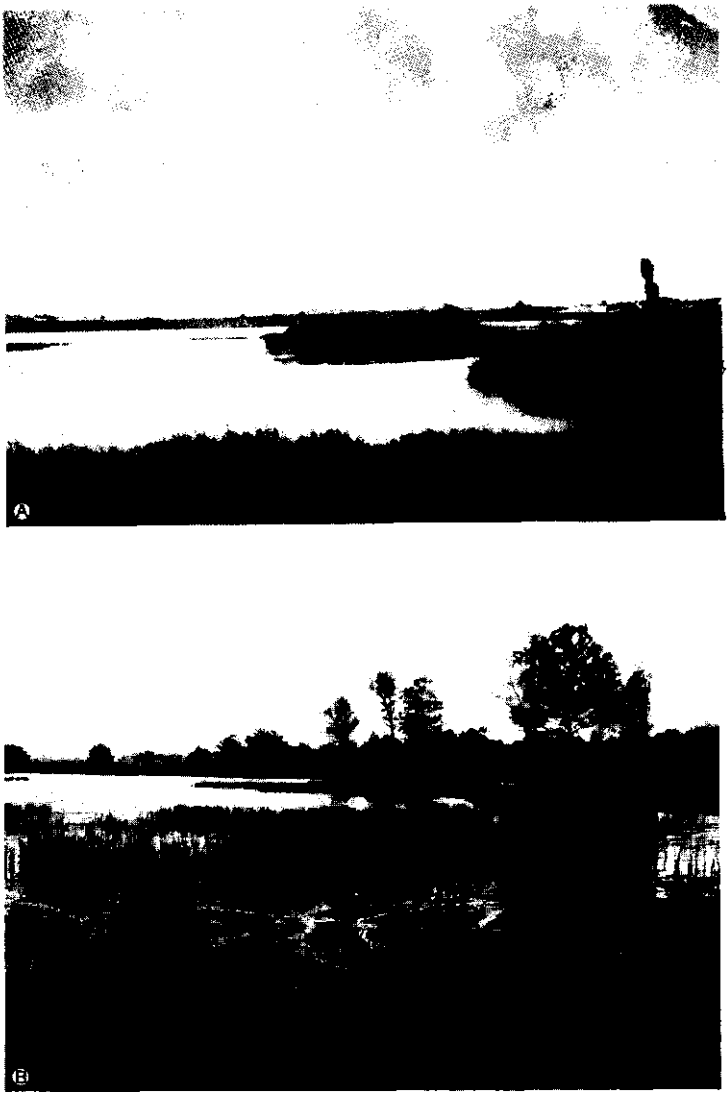
DISTRICT/ name of pool	Number	Surface area (ha) approx.	Bottom[a]	Basin	Brown or clear water[b]	Surrounding landscape ca. 1920[c]	Surrounding landscape 1978[c]
BRABANT							
Galgeven	B1	14,7	sand	probably unsealed	clear	heath with regrowth of forest	forest
Schaapsven	B2	1,4	sand	unknown	clear	heath with regrowth of forest	forest, heath with regrowth of forest
Diaconieven	B3	1,3	sand	rather sealed	clear	forest planted before 1900	forest
Brandven	B4	1,4	sand	rather sealed	clear	forest planted before 1900	forest
Achterste Goorven	B5	1,4	sand	probably unsealed	clear	forest planted before 1900	forest
Klein Aderven	B6	1,0	sand	slightly sealed	clear	heath, forest planted before 1900	forest
Middelste Wofsputven	B7	0,3	sand	unknown	brown	forest planted before 1900	forest
Groot Huisven	B8	2,9	sand	unsealed	clear	heath	heath, forest
VELUWE							
Gerritsfles	V1	5,0	sand	sealed	clear	heath, sand dunes	heath, locally with regrowth of forest; sand dunes
Kempesfles	V2	0,4	sand	sealed	clear	sand dunes with regrowth of forest	sand dunes with regrowth of forest
DRENTHE							
Kliplo	D1	0,4	sand	possibly unsealed	brown	forest planted after ca 1920, heath	forest
Poort II	D2	0,1	peat	unknown	brown	bog surrounded by forest planted after ca. 1920	bog surrounded by forest
Schurenberg	D3	1,1	sand	possibly unsealed	clear	forest	forest
Diepveen	D4	0,9	peat	unknown	brown	forest planted after ca. 1915	forest
Reeënveen	D5	0,1	peat	unknown	brown	bog surrounded by heath	bog surrounded by forest
Pool in Echtenerzand	D6	0,3	peat	unknown	clear	sand dunes, heath	sand dunes, heath

[a] Sand bottoms are often covered with detritus.
[b] Based on chemical data from table 5 (section 4.6). These do not always correspond with the actual water colour which is seen in the field. The water of D1 looks clear and that of D6 looks brown.
[c] Forests consist mainly of Scots pine, sometimes mixed with some birch and/or oak.

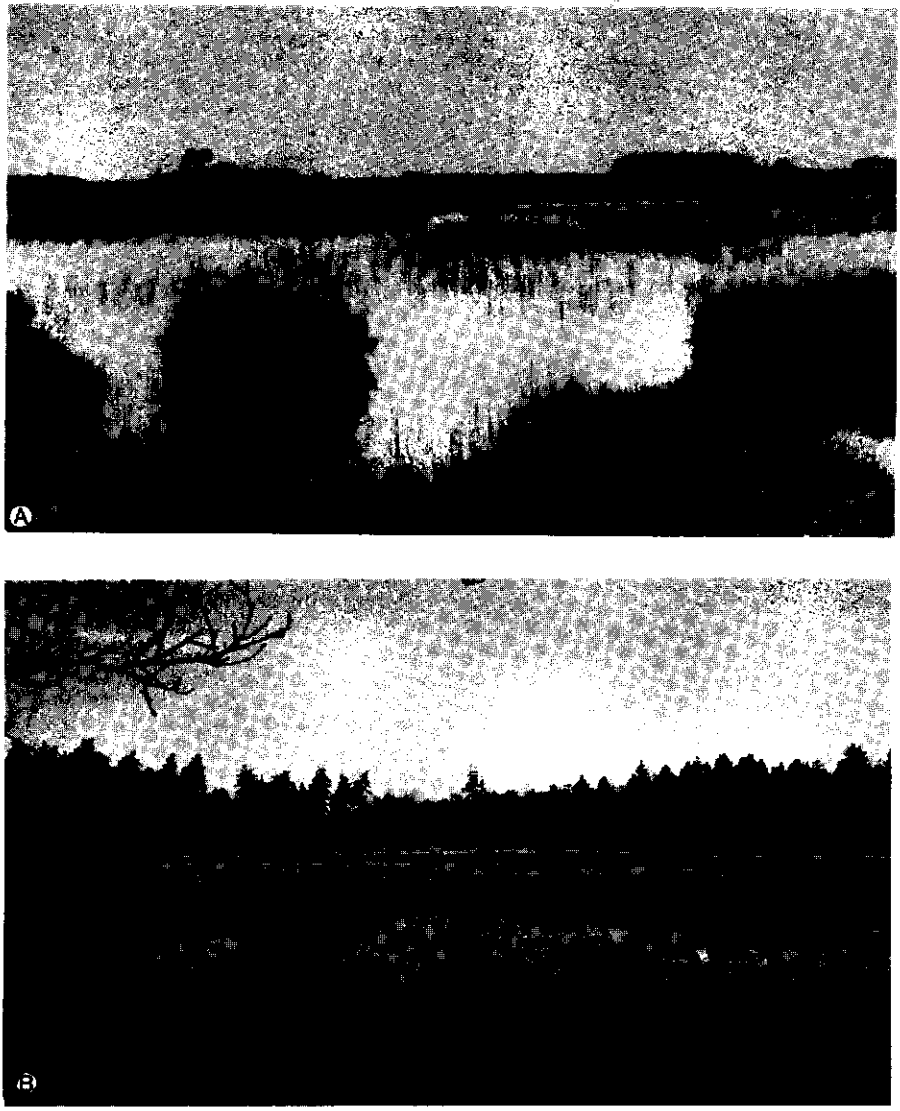
(Schimmel & Ter Hoeve 1952). Also B3 and B4 have sealed basins (Ter Hoeve 1949). B5 is aquifer fed and consequently has a larger basin than the previous moorland pools. Transitions between these extreme types occur.

D1 and *D3* have a sandy bottom. The other D-pools are tarns in small patches of bog, which are situated in depressions between inland sand dunes (Fig. 3). In some pools the peat has been excavated partially in former times.

The vegetation of most pools belongs to the oligo-dystraphentic type (Van Dam & Kooyman-van Blokland 1978). The vegetation of some of the pools in the B- and V-districts belongs to the



Figs. 2a & 2b. Part of the clear water moorland pool V1 (Gerritsfles) about 1920 (2a) and in October 1979 (2b). In 1920 the pool was in an open landscape of heath and inland sand dunes, with *Juniperus communis* as the only tree. The open water was poor in macrophytes (some *Carex rostrata*). In 1979 the pool is situated in a *Molinia caerulea* 'heath' with regrowth of *Betula pubescens* and *Pinus sylvestris*. Around the pool is a dense belt of *Juncus effusus* (foreground), followed by a girdle of *Sphagnum* spp., *Eriophorum angustifolium* and *J. bulbosus* (with duck tracks) and a zone with *C. rostrata*, colonizing the formerly open water. Fig. 2a from Thijsse (1926), Fig. 2b photo by Roel van Beek.



Figs. 3a & 3b. Part of the brown water moorland pool D4 (Diepveen) before 1920 (3a). and in May 1980 (3b). Before 1920 the pool was still in the open landscape of inland sand dunes, with *Pinus sylvestris* as the solitary tree on the left and a girdle of Scots pines around pool D3 (background right). In 1980 the pool is situated in plantations of Scots pines. Dominant aquatic macrophytes in both figures are *Carex rostrata* and *Eriophorum angustifolium*. Photo: W. Beijerinck (3a), Roel van Beek (3b).

oligotraphentic type, as described by these authors. The most prominent species of this type (*Lobelia dortmanna* L., *Isoetes lacustris* L.) were rather abundant about 1920, but are nearly extinct now.

After 1840 the heathlands and inland sand dunes, which surrounded all the moorland pools were gradually reafforested with Scots pine (*Pinus sylvestris*). The environs of B3 to B6 were already reafforested before 1900 while V1 is still in the open landscape.

3. Methods

3.1. Diatoms

Sampling, slide preparation, identification and counting have been described in detail by Van Dam & Kooyman-van Blokland (1978).

Heimans sampled the moorland pools about 1920 with a plankton net, but he certainly did not collect pure plankton. When he hauled his net, he also gathered parts of macrophytes and some bottom material, as can be seen in the samples preserved. The old and recent samples were taken in the same way. The net plankton gives a picture of the microcenoses of the whole pool, which is shallow and well mixed by wind. Sometimes squeezings of *Sphagnum* were gathered.

The most important references for identification were Van der Werff & Huls (1957–1974), Hustedt (1927–1930, 1930, 1931–1959, 1961–1966), Patrick & Reimer (1966, 1975), Cleve-Euler (1951–1955) and Foged (1977). In general the nomenclature of Hustedt (l.c.) was followed. The lanceolate *Nitzschiae* were identified according to Lange-Bertalot (1976) and Lange-Bertalot & Simonsen (1978). In each slide 400 valves were counted, while the whole slide was scanned with a low magnification (× 125) in order to list the most prominent species outside the count.

The pH-spectra were calculated with the ecological data from the literature mentioned by Van Dam & Kooyman-van Blokland (1978). Data about the geographical distribution of species were also borrowed from the literature.

3.2. Chemistry

pH and conductivity were measured on the spot with a Metrohm E 488 pH-meter and a Yellow Springs Instruments model 33 conductivity meter respectively. The pH-meter was calibrated before and after each measurement. Water samples were collected in polyethylene bottles and stored at 4 °C. Conductivity, pH, nitrite, ammonium, and bicarbonate were analysed the day after sampling; other ions within one week in the laboratory of the 'Waterleidingbedrijf Midden-Nederland'. All analyses were made in unfiltrated water, with the exception of sulfate, which was determined gravimetrically after filtration through ordinary filter paper and permanganate consumption (filtrated), which was determined after running through an asbestos filter.

Iron, calcium and magnesium were measured by atomic absorption spectrometry (AAS) using a Perkin Elmer model 703. Aluminium was analysed by flameless AAS with a Perkin Elmer model 306. Nitrate was determined according to Müller & Widemann (1955). All other determinations were carried out according to 'Nederlands Normalisatie Instituut' (1965–1968). In the laboratory conductivity was measured at room temperature and converted to conductivity at 25 °C according to Golterman (1969).

3.3. Statistics

Increase and decrease of individual species, ecological and geographical classes were tested by the Wilcoxon signed rank test (SRT), according to Lehmann (1975). Differences of these parameters between the areas (B + V) and D were tested by the Wilcoxon rank sum test (RST), according to Lehmann (1975). These tests were carried out two-tailed.

Principal component analysis was performed with a program written in APL, using an eigenvalue and eigenvector algorithm based on Jacobi's method (Wilkinson 1965). Programs for diversity analysis were written in Fortran IV and for dissimilarity analysis in APL. Batch runs were done at the CDC Cyber 72 computer of TNO (The Hague), interactive computerwork was done at the Cyber 171 of TNO.

4. Results

4.1 Taxonomy, ecology and distribution of diatom taxa

The taxonomy and ecology of freshwater diatoms

are relatively rather well known. Most European, and especially Dutch diatoms can be identified easily with the floras mentioned in section 3.1. However, some variable forms are difficult to identify. Therefore the 24 most common taxa are listed here with some annotations about their taxonomy and ecology. All taxa which could be found are listed in the appendix.

Achnanthes minutissima Kützing

A. microcephala (Kützing) Grunow is included in this taxon because H. Lange-Bertalot (pers. comm.) concludes the type material of both species to be identical. The species occurs from a pH as low as 4.4 (Besch *et al.* 1972) up to 8.4 (Schoeman 1973) and is considered to be pH-indifferent by Foged (1964) and Meriläinen (1967). This seems to be one of the few diatoms which is rather indifferent with respect to pH; in the Netherlands however, high abundances are only observed in slightly acid to alkaline waters and the species is therefore to be classified as circumneutral. Occurs only with small numbers in most of the pools studied.

Anomoeoneis exilis f. *lanceolata* Mayet

This taxon is sometimes difficult to distinguish from *A. serians* var. *brachysira* f. *thermalis* (Grunow) Hustedt, which occurred rather rarely. The latter taxon has about 27 transapical striae in 10 μm, the former one more than 30. *A. exilis* f. *lanceolata* is considered to be circumneutral by Foged (1964) and Meriläinen (1967). Renberg (1976) found this taxon abundantly in some lakes with pH 5–6. The distribution in our samples suggests that it does not thrive well in the most acid pools (pH lower than 4.5 to 5).

Anomoeoneis serians var. *brachysira* (De Brébisson) Cleve

This variety is considered to be acidophilous by many authors (*e.g.* Jørgensen 1948; Foged 1964; Meriläinen 1967). According to Hustedt (1957) rarely in the North Sea Lowlands and more common in the northern countries. Most abundant in B5, especially old samples.

Cocconeis placentula Ehrenberg

We include the varieties in the species, because these are not ecologically different from the typical species (Cholnoky 1968). The species is alkaliphilous and is very common in meso-eutrophic waters (Van der Werff & Huls 1957–1974), although it may be found in small numbers at a pH as low as 4.7 (Jørgensen 1948). In accordance with the literature data the species occurs mostly in small numbers in the pools studied.

Cymbella microcephala Grunow

Characteristic for eutrophic alkaline lakes and ponds and therefore alkaliphilous (Jørgensen 1948; Van der Werff & Huls 1957–1974). Occurred sparsely in most moorland pools, but codominant with *Achnanthes minutissima* in an old sample from B5.

Eunotia alpina (Nägeli) Hustedt

This species is sometimes difficult to distinguish from long and slender forms of *E. lunaris* (Ehrenberg) Grunow, especially when the valve has a width of ca 3 μm, which is beyond the limit of Hustedt (1931–1959), who gives a maximum width of 2.5 μm for *E. alpina*, but below the upper limit of 3.5 μm, given by Patrick & Reimer (1966) for *E. naegelii* Migula, a synonym for *E. alpina*. In case of doubt we favoured *E. alpina* when the length-to-breadth ratio was more than about 30, in accordance with both Hustedt and Patrick & Reimer.

E. alpina is acidophilous and is more common in northern and mountainous areas than in the lowlands (Jørgensen 1948; Hustedt l.c.; Cleve-Euler 1951–1955; Meriläinen 1967). Occurred frequently, but most times with low abundance in the B- and D-samples and rarely in the V-samples. Rather abundant in some recent D-samples.

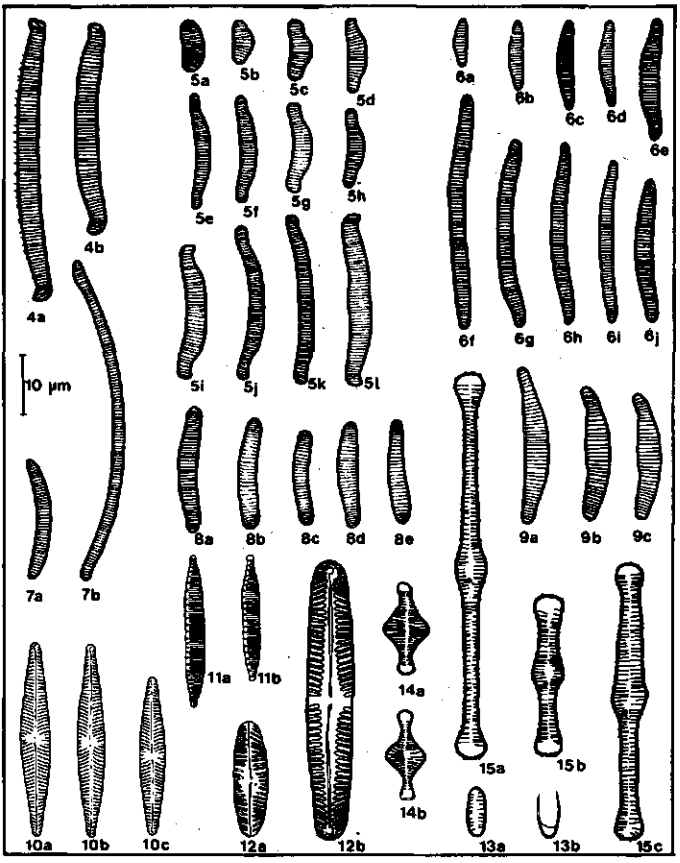
Eunotia denticulata (De Brébisson) Rabenhorst

If the small spines are present (Fig. 4a) this diatom is easy to identify. Often some spines or even all have been lost (Fig. 4b). With some experience the last forms can be distinguished by their shape and stronger silification from similar forms, like *E. exigua*.

E. denticulata is acidophilous (Meriläinen 1967; Cholnoky 1968) and has its main distribution in northern and mountainous regions. Occurred rather abundant in some old B-samples, recently only in small numbers in a few B- and D-samples.

Eunotia exigua (De Brébisson) Rabenhorst

Our concept of this highly variable species is in



Figs. 4–15. 4. *Eunotia denticulata*, 5. *E. exigua*, 6. *E. exigua/tenella* - complex, 7. *E. lunaris*, 8. *E. tenella*, 9. *E. veneris*, 10. *Navicula heimansii*, 11. *Nitzschia perminuta*, 12. *Pinnularia microstauron*, 13. *Tabellaria binalis*, 14. *T. flocculosa*, 15. *T. quadriseptata*.

accordance with Hustedt (1931–1959). The very wide range of this taxon is depicted in Fig. 5. The dimensions of these specimens are: length 6.7–28.9 µm, breadth 2.5–3.8 µm with (18) 20–24 (26) striae in 10 µm. In Fig. 6 the complex of *E. exigua* and *E. tenella* is drawn (length 7.8–39.6 µm, breadth 2.5–3.0 µm, 18–22 striae in 10 µm). This form is rather similar to *E. tenella*, but the striation is finer than is common for this species (16–20 striae in 10 µm).

E. exigua in natural waters is strongly bound to acid habitats (pools, lakes, bogs and streams) and is therefore acidobiontic (Jørgensen 1948; Symoens 1957; De Graaf 1957; Van der Werff & Huls 1957–1974; Meriläinen 1967; Cholnoky 1968). Such habitats generally have a low mineral content, but this does not mean that *E. exigua* is oligotraphentic. The species thrives equally well in acid mine drainage with a high mineral content and a high load of metals like Mn, Fe, Al, Pb, Co, Cu, Zn and

Ni (Stjerna-Pooth 1953, 1954; Besch *et al.* 1972, Hargreaves *et al.* 1975). It is probably the most resistant diatom for heavy metals. Mass occurrence is reported at a sulfate level of 1150 mg l^{-1}, while the upper limit is about 4000 mg l^{-1}. No records are made below pH = 2.5. Hargreaves *et al.* (l.c.) and Stjerna-Pooth (l.c.) mention that in such stressing environments anomalic and small forms (Fig. 5a, b) are abundant.

The species is present in all but three samples. In old samples it had a mean occurrence of 28 valves, in the recent samples it was present with a mean of 248 valves. In the recent samples the abundance (a) is significantly correlated with the sulfate concentration as follows: $a = 378 \times \log [SO_4^{2-}] - 255$ ($r^2 = 0{,}67$) and more strongly with the quotient $b = [SO_4^{2-}] / \left([SO_4^{2-}] + [Cl^-] + [HCO_3^-] \right)$. $a = 703b - 139$ ($r^2 = 0{,}89$).

Eunotia lunaris (Ehrenberg) Grunow

See also the remarks on *E. alpina*. In the counts of this taxon (Fig. 7) the forms belonging to the var. *subarcuata* (Naegeli) Grunow have been included.

E. lunaris is circumneutral, but has a slight preference for weakly acid waters (Jørgensen 1948; Hustedt 1957; Patrick & Reimer 1966). The species decreased significantly from a mean of 43 valves in the old samples to a mean of 17 valves in the recent samples.

Eunotia rhomboidea Hustedt, *E. tenella* (Grunow) Hustedt and *E. veneris* (Kützing) O. Müller

See also the remarks on *E. exigua*. The three species are closely related and not always easy to distinguish.

One of the first questions which must be solved in order to separate the species in this group properly is whether asymmetry is to be considered as a species character. Most authors depict only symmetrical forms of *E. veneris* (*e.g.* Hustedt 1931–1959), but in some cases asymmetrical forms are found (*e.g.* Manguin 1942; Meriläinen 1969). The asymmetrical specimens are rhomboid in girdle view. Van der Werff & Huls (1957–1974) picture symmetrical and asymmetrical forms from the Netherlands. Recently the asymmetrical *E. faba* f. *rhomboidea* Foged, which is commonly found mixed with symmetrical forms of this species, was described (Foged 1972).

Hustedt (1950: 435, T. 34, Fig. 28; T. 36, Fig. 34–41) describes *E. rhomboidea*, which is very similar to *E. tenella*. In Hustedt's type material of *E. rhomboidea* the asymmetry was a constant feature. However, in our material gradual transitions between the two species frequently occurred (Fig. 8). Symmetrical and asymmetrical valves were often rather abundant in the same sample. Any separation of the two 'species' would have been arbitrary. Therefore we include *E. rhomboidea* in *E. tenella*. *E. rhomboidea* cannot be maintained as a species.

Accepting that asymmetry is not a constant feature in some species the second question that must be solved is the distinction between *E. tenella* and *E. veneris*. The terminal nodules, which are removed from the ends of the valve (Fig. 9) are very characteristic for the latter species (Hustedt 1931–1959; Cleve-Euler 1951–1955; Patrick 1958). These nodules are very distinct and at some depths of focus they appear as a notch in the ventral margin (Patrick l.c.; Cleve-Euler l.c.). The ends of the valve are acute to acutely rounded (Hustedt l.c.; Patrick, l.c.). In *E. tenella* (Fig. 8) the terminal raphe nodules are close to the apex, which is rounded (Hustedt l.c.; Petersen 1950; Van der Werff & Huls 1957–1974; Patrick & Reimer 1966). As a thumb rule one may state that *E. veneris* has the nodule on about 1/8 of the valve length and *E. tenella* on about 1/12 of the valve length. The dimensions in our material are for *E. veneris:* length 18–30 μm, width 3.0–4.8 μm, 16–18 striae in 10 μm, *E. tenella:* length 10–21 μm, width 2.9–4.8 μm, 19–20 striae in 10 μm.

At least two authors do not separate the asymmetrical forms in this group according to the above mentioned criteria. Foged (1950, T. 3, Fig. 8, 9; 1977, T. 10, Fig. 27; in Berge, 1979, T. 1, Fig. 23, T. 3, Fig. 18) and Wuthrich (1975, T. 9, Fig. 1, 4–12) depict asymmetrical specimens as *E. rhomboidea* which fit in our concept of *E. veneris*. The specimens of Foged (1950, T. 3, Fig. 6, 7, 11; 1977, T. 10, Fig. 26) and Wuthrich (1975, T. 9, Fig. 2, 3) fit in our concept of *E. tenella*.

E. tenella (including *E. rhomboidea*) is acidophilous (Jørgensen 1948; Foged 1950; Hustedt 1957; Meriläinen 1967, 1969). The asymmetrical forms are found in acid, oligotrophic to dystrophic small *Sphagnum-Carex rostrata* – and *Lobelia* – lakes in north-western Germany and southern

Scandinavia (Foged 1950; Hustedt 1950; Behre 1956). Such lakes are very similar to our moorland pools. *E. veneris* is also acidophilous and has a mountainous tendency (Hustedt, 1931–1959; Jørgensen 1948; Symoens 1957; Van der Werff & Huls 1957–1974; Meriläinen 1967). The optimal pH is probably slightly higher than for *E. tenella*.

Both species were found in most samples of the study area. *E. tenella* is slightly (not significantly) less abundant in the recent samples than in the old ones. *E. veneris* decreased significantly from a mean of 57 valves in the old to three valves in the recent ones.

Fragilaria capucina Desmazières

Alkaliphilous (Jørgensen 1948; Hustedt 1957; Van der Werff & Huls 1957–1974). Occurs erratically. Rather abundant (39 valves) in a recent B1-sample.

Fragilaria virescens Ralfs

Circumneutral (Hustedt 1957; Meriläinen 1967), but best development in slightly acid waters (Schroeder 1939; Scheele 1952; Salden 1978). Most abundant in the alpine and northern areas of Europe (Hustedt 1957; Symoens 1957). This species decreased significantly in the (B + V)-samples between 1920 and 1978. It was not present in the old D-samples, but occurred rather abundantly in the recent samples D1 and D3.

Frustulia rhomboides var. *saxonica* (Rabenhorst) De Toni

This taxon is considered to be acidobiontic by Hustedt (1957) and De Graaf (1957) but acidophilous by other authors (*e.g.* Jørgensen 1948; Van der Werff & Huls 1957–1974; Meriläinen 1967). We share the first opinion, because the taxon is reported to be most abundant in humic acid waters. Cholnoky (1958), Harrison (1958) and Bennett (1968) found mass development of *F. rhomboides* var. *saxonica* in rivers that were polluted with acid mine drainage. Silfversparre (1937), Valin (1958) and Eloranta & Kettunen (1979) mention either the species or the variety, which behave ecologically very similar, to be very common in regions of sulfite discharge from wood pulp factories. Thus one would predict this taxon to increase with growing acidity of the water, like *Eunotia exigua*.

However, in the study area the mean abundance decreases significantly from 89 valves in old samples to 39 in the recent ones. It is more abundant in the samples of the Drenthian district, that is generally rich in humic acids, than in the other samples, which are from relatively humic poor water.

Navicula heimansii Van Dam & Kooyman

This species (Fig. 10) is described by Van Dam & Kooyman (in prep.). The dimensions are: length 28–35 μm, breadth 4.5–6 μm, 16–18 striae in 10 μm.

The species was not found in the V-samples. Occurs with low numbers in some B- and D-samples. Abundant in an old sample of B5 and a recent sample of D2. Possibly acidophilous. To avoid circular reasoning it would have been better to omit this species from the calculations of the pH-spectra, but this does not influence the results significantly.

Navicula subtilissima Cleve

This typical inhabitant of bogs and nutrient poor lakes is often found with *Frustulia rhomboides* var. *saxonica* and small species of *Eunotia* (Hustedt, 1961–1966) and therefore classified as acidobiontic by De Graaf (1957) and Meriläinen (1967). After having done the main body of the research it unfortunately appeared that the rather similar *Navicula hoefleri* Cholnoky was included in the counts of *N. subtilissima*. *N. hoefleri* is acidobiontic (Hustedt l.c.).

Both species decrease significantly in the B- and V-samples between 1920 and 1978. No significant changes occurred in the D-samples.

Nitzschia gracilis Hantzsch

Circumneutral according to Jørgensen (1948), Hustedt (1957), Foged (1964) and Meriläinen (1969). Occurred in low abundances in a number of samples; has a tendency to decrease from 1920 to 1978. Most abundant in an old sample of V2.

Nitzschia perminuta Grunow

Fig. 11. Valves slightly constricted in the middle, 20–25 μm long, about 3 μm wide. Transapical striae very finely punctated, about 30 in 10 μm. Keel very excentric, with 9–11 fibulae in 10 μm. Central fibulae equidistant. The specimens correspond well with those of Hustedt (1943: 231, Fig. 80, 82–87) and specimens of the type slide of Grunow (Lange-

Bertalot & Simonsen 1978: 85, Fig. 160a, b).

Considered to be alkaliphilous (Hustedt 1943). The species occurred erratically in some B-, D- and V-samples and was commoner in the old B-samples than in the recent ones. Abundant in an old sample of B5.

Pinnularia appendiculata (Agardh) Cleve

Recorded by Jørgensen (1948) as acidophilous. Cholnoky (1968) gives an optimal pH of 6,5–6,8. Regarded as circumneutral by other authors (Hustedt 1957; Foged 1964) as the species may be present in alkaline waters, but generally in low numbers (Schoeman 1973). In our experience the species has its highest abundance in acid waters and therefore we consider the taxon to be acidophilous.

Relatively scarce in the samples, but rather abundant in an old sample from V1. Decreases significantly from 1920 to 1978, especially in the D-samples.

Pinnularia microstauron (Ehrenberg) Cleve

Fig. 12. This species is extremely variable (see *e.g.* Hustedt 1930; Lund 1946; Meriläinen 1969; Foged 1974, 1977). Fig. 12b represents a typical form of the species, while Fig. 12a is related to var. *brebissonii* (Kützing) Hustedt. All intergradations between these two extremes were found.

The species and its variety are circumneutral (Hustedt 1957; Foged 1964) but have an optimal development in weakly acid waters (Jørgensen 1948; Van der Werff & Huls 1957–1974; Patrick & Reimer 1966; Cholnoky 1968).

Scattered occurrence over the whole study area, has a tendency to decrease from 1920 to 1978. Most abundant (73 valves) in V1 in 1960.

Tabellaria binalis (Ehrenberg) Grunow

Fig. 13. The Dutch material is elliptical in valve view and similar to the Danish forms (Jørgensen 1948). However, there is no reason to separate this form from the typical constricted form as figured by Hustedt (1931–1959), because there is a gradual transition from constricted to elliptical forms (Cleve-Euler 1951–1955).

T. binalis is a typical inhabitant of *Lobelia*-lakes in the former heath- and moorland area of northwestern Europe and is also found in Scandinavian *Lobelia*-lakes. Acidobiontic (Hustedt 1931–1959; Jørgensen 1948; Cleve-Euler 1951–1955). The relative abundance in some cores from acidified Scandinavian lakes increased during the last decennia (Miller 1973; Berge 1979).

Regularly present in the old B-samples. Mass occurrence in B8. Recently only a few frustules in the study are.

Tabellaria flocculosa (Roth) Kützing

Fig. 14. Acidophilous (Jørgensen 1948; Hustedt 1957, Van der Werff & Huls 1957–1974). Patrick & Reimer (1966) state that the short individuals (as in our figure) are more often found in acid water of bogs and ponds, whereas the longer ones seem to be more often found in oligotrophic to mesotrophic water.

In rather small quantities in most of the samples, rather abundant in the old samples from B2 and D1.

Tabellaria quadriseptata Knudson

Fig. 15. This species is often confused with *T. fenestrata* (Lyngbye) Kützing (see *e.g.* Van Dam & Kooyman-van Blokland 1978). Characteristic features of *T. quadriseptata* are: the gradually tapering terminal inflations, the peripheral position of the mucilage pore and the marginal spines, which are visible in the light microscope (Knudson 1952; Patrick & Reimer 1966; Koppen 1975).

The species is confined to acid (dystrophic) water with a low mineral content (Knudson 1954; Florin 1957; Patrick & Reimer l.c.; Plinski & Witek 1976; Sims 1978) and we therefore classify the species as acidobiontic. In the study area the species was present in nearly all samples and had a tendency to decrease in the B-samples from 1920 to 1978.

In total 194 species and varieties, belonging to 36 genera were found. All taxa are listed in the appendix, together with their pH-class and notes about geographical distribution. The distribution of 24 taxa occurring at least with 20 valves in one sample, is listed in Table 2. The samples are in the order of their score on the first principal component, and the species in the order of their loadings on this component (see section 4.5).

The increase or decrease of the species from 1920 to 1978 was tested by SRT. When two or more samples of one pool at one moment were available, one sample was drawn at random. The selected samples are indicated in Table 2. The species with a

Table 2. Number of valves per species in each sample. + = observed outside the count, - = not observed, BA = *Batrachospermum*-squeezing, BM = bottom mud, BS = bottom sand, EP = epiphytes from *Littorella uniflora, Lobelia dortmanna* or *Juncus bulbosus*, NP = net plankton, SP = sedimentation plankton, SQ = squeezing of *Juncus bulbosus* and *Sphagnum* spec., SS = *Sphagnum*-squeezing, UT = squeezing of *Utricularia minor*. Closed symbols: old samples used for pairwise comparison, open symbols: recent samples used for pairwise comparison.

pairwise comparison	type of sample	month and year	pool number	*Frustulia rhomboides* var. *saxonica*	*Eunotia veneris*	*Eunotia lunaris*	*Eunotia tenella*	*Tabellaria quadriseptata*	*Navicula subtilissima*	*Tabellaria binalis*	*Navicula heimansii*	*Tabellaria flocculosa*	*Anomoeoneis exilis* f. *lanceolata*	*Eunotia denticulata*	*Achnanthes minutissima*	*Eunotia alpina*	*Fragilaria virescens*	*Cymbella microcephala*	*Pinnularia appendiculata*	*Pinnularia microstauron*	*Nitzschia gracilis*	*Nitzschia perminuta*	*Fragilaria capucina*	*Eunotia tenella/ exigua* complex	*Cocconeis placentula*	*Anomoeoneis serians* var. *brachysira*	*Eunotia exigua*
●	NP	8.22	D3	232	63	36	2	28	7	-	9	7	1	-	-	-	-	-	-	1	2	-	-	-	-	-	1
■	NP	8.33	D6	239	47	50	6	10	+	..	1	-	..	-	4	-	-	-	7	16	-	-	-	7	-	-	1
	BA	6.16	V1	66	9	310	..	-	14	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
■	NP	8.24	D4	33	255	55	1	-	7	-	-	+	..	-	9	4	-	1	+	-	-	-	-	-	-	-	2
	NP	6.16	V1	18	289	45	17	2	3	-	-	13	-	-	-	+	+	-	-	+	-	-	+	-	-	-	6
▼	NP	7.18	V2	41	187	13	-	28	60	-	-	9	2	-	3	-	-	-	-	-	25	-	-	-	-	-	3
●	NP	8.24	D1	56	96	35	33	22	61	-	2	72	1	-	10	-	-	-	+	..	-	-	+	-	-	-	+
■	NP	6.29	D5	283	+	56	+	-	-	-	+	+	-	-	-	+	-	-	-	-	-	1	-	17	-	-	26
	NP	10.21	B5E	113	41	14	4	70	22	..	92	1	17	+	2	11	-	-	+	-	+	-	-	-	-	-	3
●	NP	8.22	B7	122	-	10	8	75	2	-	1	+	-	156	5	10	-	-	-	-	1	-	-	-	+	-	4
●	NP	7.25	B2	50	39	93	8	58	68	-	-	53	-	-	3	1	2	1	-	+	6	-	..	-	-	-	7
	NP	7.18	V1	25	76	60	114	3	52	-	-	10	34	-	-	-	-	-	-	2	4	-	-	-	-	-	6
□	NP	11.78	D5	202	4	42	3	4	-	1	-	+	-	-	6	109	-	-	-	-	-	-	1	-	3	-	19
	EP	7.29	B8	3	101	-	6	13	1	252	-	1	-	-	-	+	4	-	-	1	-	-	-	-	-	-	3
	EP	7.29	B8	17	53	3	3	22	5	272	3	3	-	-	+	+	1	+	-	+	+	-	-	-	-	-	1
■	NP	8.24	D2	180	88	29	9	29	+	-	-	-	-	-	1	4	-	-	+	1	-	-	-	-	21	-	30
▼	NP	7.18	V1	24	27	99	72	-	65	-	-	23	36	-	8	-	1	-	-	6	6	-	-	-	-	-	5
	NP	8.50	B5B	33	59	22	16	21	11	-	9	5	44	-	6	-	74	4	-	2	5	1	-	-	-	39	-
	NP	9.19	B6	87	11	1	16	131	34	-	7	2	1	55	-	14	1	-	-	+	1	-	-	-	-	4	10
	UT	7.16	V1	24	54	87	105	-	1	-	-	+	-	-	-	1	-	-	90	2	-	-	-	4	-	-	11
	NP	6.52	B5A	10	27	132	33	2	2	-	4	3	11	-	44	5	13	4	3	+	6	1	1	-	4	-	6
□	NP	11.78	D1	28	20	10	31	4	114	-	98	9	22	-	-	-	30	-	-	+	1	-	-	-	+	-	1
	NP	9.50	V1	36	80	10	203	10	6	-	-	15	6	-	-	-	-	-	+	1	-	-	-	-	+	-	16
●	NP	9.20	B6	88	7	4	15	221	8	+	-	-	-	25	-	7	-	-	1	+	-	-	-	-	-	-	16
□	NP	11.78	D2	99	2	41	25	135	8	-	..	1	..	3	5	42	-	-	+	-	1	-	-	-	+	-	19
●	NP	9.26	B5B	29	5	4	6	1	4	-	120	6	53	-	2	2	64	3	+	+	6	48	-	-	+	6	-
●	NP	6.19	B1	52	2	3	83	33	2	75	-	21	-	-	8	3	-	-	-	2	1	+	39	-	-	-	15
	BM	7.18	V1	20	-	65	131	9	61	-	-	20	33	-	1	-	-	-	-	-	+	-	-	-	-	-	18
	NP	7.60	V1	49	37	25	159	7	2	+	-	10	3	-	3	-	-	-	1	73	-	-	-	-	-	-	24
	NP	12.19	B5A	3	+	+	1	1	1	-	+	1	38	4	189	2	-	145	-	-	-	+	2	-	-	-	10
	NP	9.50	V1	121	43	7	113	10	-	+	-	17	+	-	1	1	-	-	-	-	-	-	-	-	+	-	86

Table 2. (Continued).

pairwise comparison	type of sample	month and year	pool number	*Frustulia rhomboides* var. *saxonica*	*Eunotia veneris*	*Eunotia lunaris*	*Eunotia tenella*	*Tabellaria quadrisepiata*	*Navicula subtilissima*	*Tabellaria binalis*	*Navicula heimansii*	*Tabellaria flocculosa*	*Anomoeoneis exilis* f. *lanceolata*	*Eunotia denticulata*	*Achnanthes minutissima*	*Eunotia alpina*	*Fragilaria virescens*	*Cymbella microcephala*	*Pinnularia appendiculata*	*Pinnularia microstauron*	*Nitzschia gracilis*	*Nitzschia perminuta*	*Fragilaria capucina*	*Eunotia tenella* / *exigua* complex	*Cocconeis placentula*	*Anomoeoneis serians* var. *brachysira*	*Eunotia exigua*	
□	NP	11.78	D4	97	1	70	1	90	2	–	1	1	–	–	2	4	–	–	–	–	–	1	–	–	6	–	111	
□	NP	11.78	D3	48	8	11	113	21	16	–	12	5	4	–	–	–	4	–	–	+	10	1	–	5	–	+	111	
●	NP	6.16	B3	6	+	+	29	196	+	+	1	+	–	–	+	–	1	–	–	+	–	2	–	–	+	–	163	
○	NP	11.78	B2	14	+	+	+	143	–	–	–	5	–	–	8	–	+	2	1	1	–	–	–	–	2	–	174	
●	NP	4.26	B4	33	–	2	45	13	2	+	8	1	–	24	+	26	1	–	–	7	–	–	–	23	–	–	177	
	NP	7.73	V2	50	40	12	44	18	1	–	–	2	–	–	–	10	–	–	–	3	6	–	–	–	–	–	210	
	NP	11.78	B5A	19	5	4	21	19	12	–	+	2	7	–	1	–	20	+	–	–	–	+	–	–	+	19	256	
	BM	11.77	V1	11	12	5	52	11	6	1	–	4	11	–	–	–	–	–	–	1	1	–	–	–	–	–	272	
○	NP	11.78	B7	26	2	6	46	10	1	–	–	2	–	–	5	3	+	–	–	1	–	–	–	–	2	+	276	
	NP	11.78	B5E	12	12	2	31	12	4	–	3	1	4	+	–	–	+	–	–	1	–	–	–	–	+	13	291	
□	NP	11.78	D6	62	1	1	13	2	–	–	+	1	–	+	2	+	–	–	–	–	–	–	–	–	+	+	311	
○	NP	11.78	B1	21	–	+	15	+	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	2	–	307	
○	SQ	11.78	B8	6	+	+	3	+	–	–		–	–	–	21	–	–	–	–	+	–	–	1	–	1	–	343	
○	NP	11.78	B5B	5	3	3	5	5	+	–	2	1	4		+	–	7	1	–	+	+	2	–	–	+	3	352	
	NP	11.78	V1	–	6	1	10	5	2	1	–	3	2	–	2	–	–	–	–	–	–	2	–	–	–	–	355	
	BS	11.78	V1	5	2	–	19	5	–	–	–	2	+	–	–	–	–	–	+	+	–	–	–	–	–	–	364	
	NP	11.77	V1	7	–	3	7	1	1	–	–	+	6	–	1	–	–	–	–	2	–	–	–	–	+	–	371	
	NP	11.78	B8	2	+	+	12	8	–	–	–	–	–	–	6	–	–	–	–	+	–	–	+	–	+	–	372	
○	NP	11.78	B4	3	+	+	4	1	–	–	1	+	–	–	–	+	+	–	–	+	–	–	–	–	–	–	375	
	NP	10.65	V1	1	+	–	7	15	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	376	
	NP	11.78	V1	3	2	+	11	+	2	–	–	2	–	–	+	–	–	–	+	+	–	–	–	–	–	–	378	
○	SS	11.78	B3	14	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	386	
○	NP	11.78	B6	+	3		5	+	1	+	–	1	+	–	–	1	–	–	+	+	–	–	–	–	+	+	385	
	SP	11.78	V1	1	1	–	4	+	–	–	–	+	–	–	–	–	–	–	–	+	–	–	–	–	–	–	394	
▽	NP	11.77	V2	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	400	
▽	NP	11.78	V1	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	400	

Table 3. Species which significantly changed in abundance between 1920 and 1978.

Increased	P	Decreased	P
Anomoeoneis exilis	0.026	*Eunotia lunaris*	0.016
Cocconeis placentula	0.036	*Eunotia veneris*	0.034
Cyclotella meneghiniana	0.025	*Frustulia rhomboides*	
Eunotia exigua	0.001	var. *saxonica*	0.004
Eunotia polydentula	0.046	*Surirella arctissima*	0.008
Fragilaria vaucheriae	0.007		
Navicula minima	0.042		
Nitzschia gandersheimiensis	0.024		
Rhoicosphenia curvata	0.029		
Stauroneis phoenicenteron	0.044		

significant change in distribution are listed in Table 3. *Eunotia denticulata, Fragilaria virescens* and *Tabellaria binalis* occurred rather abundantly in some pools about 1920 and were very rare in 1978, when they occurred sparsely in some pools in which they were absent before. As the test is based on ranking, the remarkable decrease is not reflected by the results of the test.

It is noticeable that most of the increased species are typical for eutrophic, circumneutral or alkaline waters. Only *Eunotia polydentula* and *E. exigua* are species of acid water. From the description of the autecology of the latter species it appears that also this species is often found in eutrophic waters. All the decreased species are indicative for an acid, oligo-mesotrophic environment.

In each sample the abundance of the species with an alpine, boreo-alpine, boreal or mountainous distribution in Europe (marked by M in the appendix) was added. These abundances were compared pairwise. Again with the SRT and the hypothesis that there was no change in the abundance of M-species there is a significant ($P < 0.01$) decrease of these species. The optimal development of M-species is in slightly acid water that is poor to moderately poor in nutrients. A decline of these species means either a deviation from the optimal pH or eutrophication or both.

4.2 pH-spectra

pH-spectra of one old and one recent sample of each moorland pool are given in Fig. 16. When two or more samples of one pool in the same period were available, one sample was drawn at random.

Nygaard's (1959) method to estimate the pH quantitatively from the pH-spectrum according to Hustedt (1939) was gauged in Finnish lakes by Meriläinen (1967). From the latter publication it appears that Nygaard's indices α, ϵ and ω are not suitable for the determination of the pH from pH-spectra when the pH is less than about 5.

Nevertheless it is useful to summarize the whole pH-spectrum in one number, say R. If we assign the numbers 1, 2, 3, 4 and 5 to the pH-classes acidobiontic, acidophilous, circumneutral, alkaliphilous and alkalibiontic respectively and suppose the number of valves in each of these classes to be n_1, n_2, n_3, n_4 and n_5 respectively, then $R = \Sigma i n_i / \Sigma n_i$. The values for R_o and R_r (o = old, r = recent) are printed in the top right corner of each diagram in Fig. 16.

All B- and V-pools acidified more or less. In pool B8 R decreases only very slightly. However, acidobiontic species increase considerably in this pool too, at the cost of acidophilous species. This increase is counterbalanced by an increase of species from neutral or alkaline, eutrophic waters (*e.g. Achnanthes lanceolata, Navicula seminulum* and *Rhoicosphenia curvata*). The recent pH-spectra of B8, B2 and B4 are distinctly bimodal.

All old B- and V-spectra are unimodal. This may indicate that the water contains enough nutrients for eutraphentic species, but these cannot thrive well because of the acid conditions.

Old and recent pH-spectra of D1 and D2 are very similar: apparently no acidification occurred. In D3 and D5 the spectra shift to the right. These pools are now less acid than in earlier days. D4 and D6 are more acid now than in former times.

The differences R_o-R_r were tested by SRT. In all pools together R decreased significantly ($P = 0.002$). In the group (B + V) the decrease is even more significant ($P = 0.001$), but not in D ($P = 0.34$). From RST it appears that R_o differs not significantly between the two groups and that R_r is significantly lower in (B + V) than in D ($P < 0.05$).

The old pH-spectra are more diverse than the recent ones. The latter ones are very similar. In earlier days the diversity of pH-spectra was greater within the (B + V)-group than within the D-group. Now the situation is reversed.

For the present it is not possible to estimate the pH with R. From visual inspection of Fig. 16 one gets the impression that the pH has fallen 1 to 2

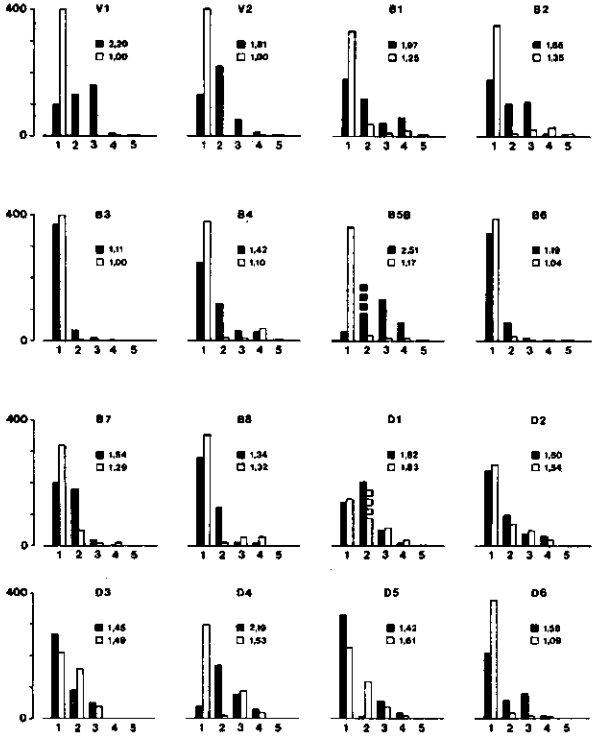


Fig. 16. Histograms of pH-spectra. Ordinate: number of valves in each pH-class. Abscissa: pH-classes (1 = acidobiontic, 2 = acidophilous, 3 = circumneutral, 4 = alkaliphilous, 5 = alkalibiontic). Black bars ca 1920, white bars 1978. Broken bars represent *Navicula heimansii* of which the ecological position is still uncertain. In top right corner of each diagram R_0 (upper number) and R_r (lower number).

points in the most acidified pools (V1, V2 and B5). In the other B- and V-pools the decline is 0.5 to 1 point.

From several pools more than one recent and old sample is available. For B5 and V1 the pH-spectra are given in Fig. 17 and 18. Data for the period between ca 1920 and 1978 have been included in these figures too. The stations A, B and E in B5 are arranged in a transect from west to east. In about 1920 there was a clear pH-gradient in this direction. This gradient seems to persist until ca 1950. However, this is difficult to assess because of the lack of data at station B. In 1950 the pH was already lower than in 1920. The decrease continues after 1950. Now the differences between the stations are definitely less distinct than in 1920.

The same process can be observed in V1 (Fig. 18). In contrast with B5, the exact localities of the old sample stations are not known. It is sure that these samples were taken at different places, just as in 1977 and 1978. The increase of acidobiontic species is obvious. There seems to be a turnover point between 1960 and 1965. However, these data have to be interpreted cautiously because of the high variability of the abundance of acidobiontic diatoms in the middle-period.

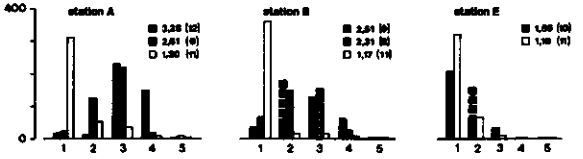


Fig. 17. Histograms of pH-spectra for three stations in B5. Dotted bars ca 1950. Central number in top right corner of each diagram: R_{1950}. Between parentheses month of sampling. Other symbols as in Fig. 16.

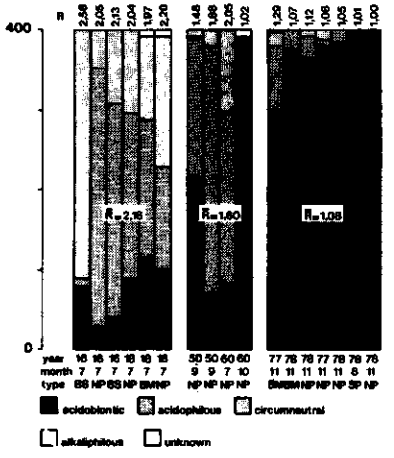


Fig. 18. Histograms of pH-spectra for all samples from V1 (1916–1978). Each column represents one sample. The number of valves in each sample is indicated. $\bar{R}$ is the mean R for each period. Type of sample: see Table 1.

From Fig. 17 and 18 it also appears that seasonal variations are less important than are changes in the long run.

4.3 Diversity

Indices of diversity are meant to summarize the species-abundance distribution in one number. Some indices, *e.g.* the number of species in the sample, are especially susceptible to the contribution of rare species; others, *e.g.* Simpson's (1949) measure of concentration, are more sensitive to the contribution of the most abundant species. The family of diversity indices suggested by Hill (1973) makes it possible to examine these different aspects of the vector of abundances of a sample in a systematical way (Kempton 1979). Hill's family is defined by $\Delta_a = (\Sigma \pi_i^a)^{1/(1-a)}$, where $(\pi_1, \pi_2, \ldots, \pi_T)$ is the vector of relative abundances of species in the sample; a may be any real number. Some special cases are:

$\Delta_{-\infty}$	: the reciprocal of the relative abundance of the rarest species in the sample
$\Delta_0 = T$	: the number of species in the sample
$\Delta_1 = e^H$	: $H = -\Sigma \pi_i \ln \pi_i$, the Shannon-index
$\Sigma_2 = (\Sigma \pi_i^2)^{-1}$	: the reciprocal of Simpson's measure of concentration
Δ_∞	: the reciprocal of the relative abundance of the commonest species (the dominance index of Berger & Parker, 1970).

Thus Δ_a becomes more sensitive for the contribution of dominant species when a increases. Low values of a emphasize the richness component of diversity, high values of a stress the evenness component.

The median diversities of old and recent samples from the (B + V)-pools and D-pools are given in Fig. 19. In addition to Δ_a also S, *i.e.* the number of all the species recorded in the inspected sample, is given. It appears that S within the group (B + V) was greater in 1978 than in 1920, although the difference is not significant ($P = 0.09$, SRT). For $a \geqslant 0$ Δ_a significantly decreases in this group ($P < 0.01$). Δ_a (including S) decreases in D for all a, but not significantly ($P > 0.25$). From RST it appears that the diversity of the groups (B + V) and D did not significantly differ in 1920, but in 1978 the diversity in (B + V) is smaller than in D for $a \geqslant 0.25$ ($P < 0.05$).

From the stations B5A and B5B samples are available from ca 1950 (Table 2). The diversities for all a (including S) are higher in 1978 than about

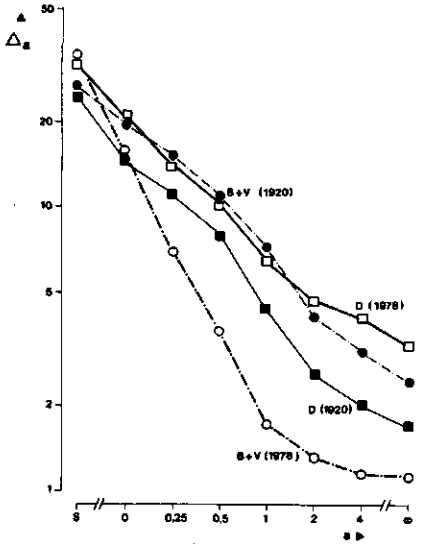


Fig. 19. Logarithmic plot of median Hill diversity (Δ_a). S = all species observed in slide.

1920. The diversities of the period in between are higher than in other periods. In V1 several samples for all periods are available (Table 2). In this pool Δ_a gradually declines with time. The differences between ca 1920 and 1978 are significant for $a \geq 0.50$ ($P < 0.05$, RST).

4.4 Dissimilarity

As Dyer (1978) stresses, a major drawback to most applications of (dis)similarity indices has been the general inadequacy or complete omission of formal statistical analysis. He develops a method to estimate the variance of the mean of dissimilarities by allowing for the covariance between dissimilarities that have one sample in common. This method will be applied on two measures which differ in their sensitivity for the contribution of rare species.

The number of species in- and outside the count that is common to both samples in examination, say P, weighs all the species, regardless of their abundance, equally well. Strictly speaking P is a similarity measure, but the statistics can also be used in this case (Dyer 1978). Q is the index as suggested by Dyer (1978, formula 13), which is related to Simpson's (1949) measure of concentration and stresses the contribution of the dominant species. Q has an expected value of zero if the organisms are dispersed randomly.

Four different kinds of mean dissimilarities are of interest. They are the mean (o) of the dissimilarities of old samples, with a typical element denoted by d_{KL}, the mean (r) of the dissimilarities of recent samples, with a typical element denoted by d_{kl}, the mean (o-r) of the changes in dissimilarity, *i.e.* the differences $d_{KL} - d_{kl}$ for all K, k, L and l, and the mean (z) of the values $d_{Kl} + d_{kL} - d_{kl} - d_{KL}$ for all K, k, L and l. z may be interpretated as the shift of the centroid of species composition with time. The variances of these means are calculated by Dyer's method and tests are based on these variances.

The results of the calculations for the 16 pairs of samples which are marked in Table 2 are given in Table 4. Let us denote the area by a superscript and the group by a subscript. P^{B+V} does not change significantly with time, because $\hat{\beta}^{B+V}_{o-r}$ is smaller than twice the square root of its variance. Nevertheless there are changes, because $(\hat{\sigma}^2)^{B+V}_r > (\hat{\sigma}^2)^{B+V}_o$. The increase of $\hat{\beta}^{B+V}$ with time indicates that two dissimilarities with one sample in common are *more interdependent in the recent* (B + V)-samples than in the old (B + V)-samples. Besides, there is a significant change in the place of the centroid of species composition. For P no significant changes are found in the area D.

The Dyer dissimilarity Q decreases significantly in the (B + V)-pools. Also z is significant. Q does not significantly increase in the D-pools, but the change in species composition is significant.

Thus, changes are most obvious in Q, which stresses the differences which are seen at a rather rough inspection of the slides. The differences fade away with more careful inspection, as is the case with P.

4.5 Principal component analysis

Principal component analysis (PCA) visualizes the position of diatom samples in the vector space of species in a graphical display. Dissimilarity and diversity can approximately be read from the graph (Ter Braak, in prep.).

Table 4. Dissimilarity statistics.

$\hat{\beta}$: estimate of mean dissimilarity (Dyer 1978, formula 9)
var ($\hat{\beta}$): estimate of variance of $\hat{\beta}$ (Dyer 1978, formula 12)
$\hat{\sigma}^2$: variance of the dissimilarities (Dyer 1978, formula 10)
$\hat{\rho}$: estimate of covariance between two dissimilarities which have one sample in common
*: significant at $P < 0.05$ level

Area	Group	$\hat{\beta}$	Var ($\hat{\beta}$)	$\hat{\sigma}^2$	$\hat{\rho}$
	P: number of species in common				
B + V	o	13.36	1.304	7.12	1.84
	r	10.98	6.427	32.11	9.24
	o-r	2.37	5.614	31.75	7.84
	z	-2.27*	1.084	10.72	1.23
D	o	12.40	6.382	15.44	2.86
	r	16.67	3.067	13.02	0.67
	o-r	-4.27	8.271	26.86	2.85
	z	1.93	-0.040(1.52)[a]	9.13	-1.17
	Q: Dyer dissimilarity				
B + V	o	0.20	0.0011	0.0071	0.0016
	r	0.05	0.0010	0.0048	0.0015
	o-r	0.15*	0.0032	0.0160	0.0045
	z	0.59*	0.0115	0.0498	0.0170
D	o	0.13	0.0033	0.0125	0.0009
	r	0.18	0.0038	0.0102	0.0016
	o-r	-0.05	0.0095	0.0293	0.0035
	z	0.10*	0.0022	0.0113	0.0002

[a] between parentheses var ($\hat{\beta}$) with the assumption that $\hat{\rho} = 0$

The Dyer dissimilarity Q (section 4.4) is an unbiased estimator for half the squared Euclidian distance, that is used as a distance measure in PCA. As the real Q is approximated rather well by projection of the samples in a few dimensions it is possible to estimate Q from the graph.

A diatom assemblage that is poor in species and dominated by one or two species will be far from the origin in the vector space of species. A diverse assemblage, with many species in low abundances will be close to the origin. In noncentred PCA the distance of the sample to the origin of the graph is a measure for Simpson's (1949) measure of concentration, *i.e.* the inverse of Hill's (1973) index for $a = 2$. Thus Δ_2 can be read approximately from the graph for each sample. In centred PCA, however, the origin of the graph is not the real origin of the vector space of species, but the centroid (the point representing the mean abundance of each species). The real origin can be calculated and added to the graph.

To examine which species are responsible for the position of the samples in the vector space of species the loadings of the species are plotted simultaneously with the scores of the samples in a 'biplot' (Gabriel 1971). The loadings are scaled to a sum of squares of unity, while the scores are scaled to a sum of squares equal to the corresponding eigenvalues. These scalings correspond to an Euclidian distance biplot, which can be interpretated in terms of species counts, the diversity index Δ_2, and the Dyer dissimilarity Q.

PCA was done according to Orloci (1966), after centering the species, but without any further standardization. Only the 24 species that are present with at least 20 valves in one of the 57 samples (Table 1) were used. According to Whittaker & Gauch (1978) it is a corollary that, for a vegetation fairly rich in species, reduction of the number of species used for ordination only slightly reduces ordination efficiency. In our case this can also be argued theoretically. From section 4.4 it appears that differences are best seen with a dissimilarity measure that is not sensitive for the contribution of rare species, *i.e.* the Dyer dissimilarity Q. As already noted, the Euclidian distance, used in PCA, has a simple relationship with Q.

The purpose of our ordination is not only to visualize the data of diatom counts in a convenient graph, but also to correlate principal components with environmental parameters. As species often have a non-linear relationship with environmental parameters a simple Gaussian ordination, based on an eigenvector method and a suitable data transformation (Kooijman 1977) was carried out.

The first and most important principal components of both ordinations are very similar; the other principal components are different. Because the first component has a very significant correlation with acidification, as will be discussed in the next section, only the linear PCA is dealt with here.

The results are given in Fig. 20. Threedimensionally the ordination has about the shape of a

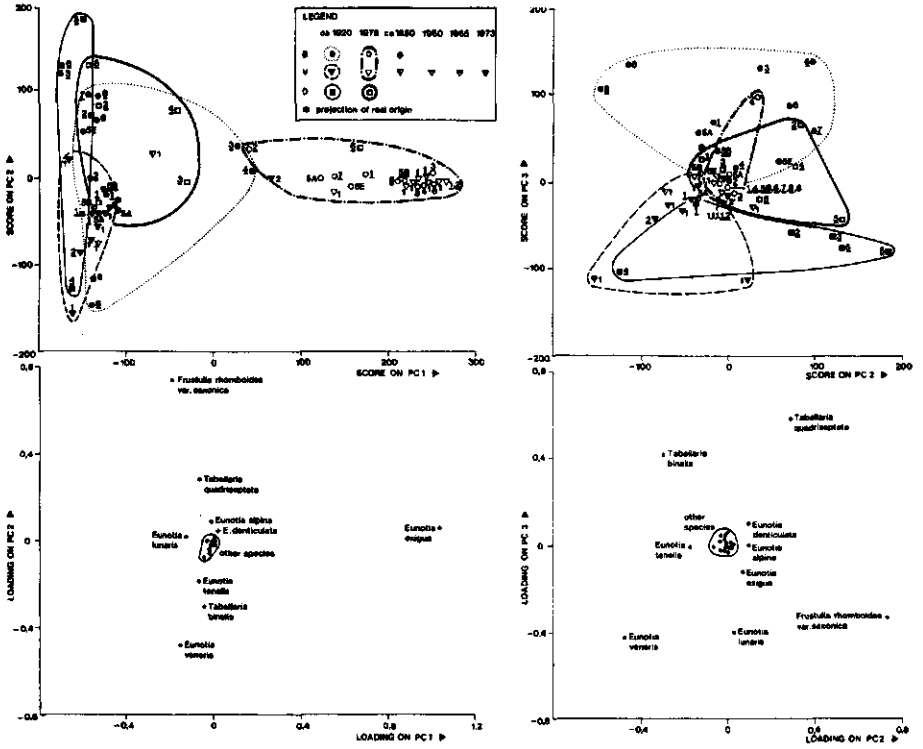


Fig. 20. Biplots of principal component analysis. Samples used for pairwise comparisons are underlined.

toad-stool. In the first two dimensions we look at the stem and the side-projection of the umbrella; in the second and third dimension we look at the bottom of the umbrella, in which the stem is projected as only a small circle. The first principal component (PC 1) represents 61.3% of total variance; PC 2 and PC 3 represent 9.1 and 6.3% of total variance respectively. Thus Fig. 20 explains 76.7% of the total variance. The projection of the real origin is indicated by ★ in the plane of PC 1 and PC 2. To approximate the inverse of Δ_2 one has to measure the distance of each sample to the point at a distance of 116.2 units from ★ perpendicular above the plane of the paper. The distance of the real origin to the space of PC 1, 2 and 3 is 110.0 units.

PC 1 completely separates the recent (B + V)-samples from the old ones, mainly by *Eunotia exigua*, which is dominant in the modern samples (at least 174 valves in each sample). This cluster includes D6. The old B3- and B4-samples are very close to the recent (B + V)-cluster. All other old B-and V-samples have a low score on PC 1, and thus a low abundance of *E. exigua*. It is easily seen that the species composition differs among these samples, *e.g.* B8 has a relatively high proportion of *E. veneris* and *Tabellaria binalis*, while B6 and B7 are rich in *T. quadriseptata* and *Frustulia rhomboides* var. *saxonica*. The cluster of old V-samples partly overlaps the old B-cluster in the first two dimensions, but is separated in the third dimension.

The old V-samples are relatively rich in *Eunotia lunaris, E. tenella* and *E. veneris*. Old B-samples are differentiated by *Tabellaria binalis* and *T. quadriseptata*.

The recent (B + V)-samples are very close to each other, so that their mean Dyer dissimilarity is low. In contrast, the old (B + V)-samples are more spread out, so that their mean Dyer dissimilarity is high (see also Table 4). Above that there is a considerable shift of the centroid of the cluster with time.

All samples with a high abundance of *Eunotia exigua* are far from the real origin and thus have a low diversity. This is also the case for other samples with dominance of other species, *e.g.* old B6 with *Tabellaria quadriseptata*, old B8 with *T. binalis* and an old V1-sample with *E. veneris*. Old (B + V)-samples are closer to the origin than recent ones, therefore the former ones are more diverse.

Also recent D-samples have a higher score on PC 1, and thus a higher proportion of *E. exigua*, than old D-samples. There is a shift on PC 2 and PC 3 too, which is caused by a decrease of *E. veneris* and *Frustulia rhomboides* var. *saxonica*. Also *Tabellaria quadriseptata* and *Eunotia tenella* contribute to the move of the D-cluster with time. As the intersample distances within the two D-clusters are about the same, the Dyer dissimilarity does not change with time, although the shift of the centroid of the cluster is significant (see also Table 4). The recent D-samples have another direction to the origin than the old ones, but their distance from the origin does not change (with the exception of D6); neither does diversity.

Furthermore it is interesting to see that the samples of V1 and B5 from about 1950 are very close to the old samples. The V1-sample of 1965 is in the cluster of recent samples, while the V1-sample of 1960 was still close to the old samples. So, major changes apparently occurred after this year. Also note the increase of *Eunotia exigua* in V2 between 1973 and 1978, which will be discussed in section 5.2.

The general conclusions from PCA are that the variation within recent samples, especially in the Veluwe- and Brabant-districts, totally differs from the old variation. While there was a great dissimilarity between the old samples, with generally high diversities, there is only a rather small dissimilarity in the recent samples, with low diversities. The variation that is left, is mainly caused by differences in the relative abundance of only one single species: *Eunotia exigua*. In the Drenthian samples there is also a shift in species composition, among other things an increase of *E. exigua*, but no clear change in dissimilarity and diversity.

4.6 Chemistry and diatoms

The results of chemical analyses are given in Table 5. The analyses of some old samples from moorland pools and some measurements of precipitation chemistry have been included. This table gives not only the absolute amounts of major ions, but also some ratios. The relative composition of the cations Ca^{2+}, Mg^{2+}, $(Na^{+} + K^{+})$ and the anions HCO_3^-, SO_4^{2-} and Cl^- is visualized in Fig. 21. This diagram comprises cation- and anion-triangles, which are combined for economy of space.

The old pH-measurements have been made in the field by colorometry. Almer *et al.* (1974) report that measurements with color-indicator solutions are close to electrometric measurements, the color-indicator values seldom being more than two-tenths of a unit higher. Thus the magnitude of the old measurements is correct. Calculated pH-values from the CO_2-HCO_3^- equilibrium (see *e.g.* Golterman 1969) are 6.5 and 6.8 for the old samples from B6 and B5B respectively. This is not in agreement with the direct measurements, which are about 4.5 and 5.5 respectively. CO_2 was measured in the field and HCO_3^- was determined after one or more days in the laboratory. pH and the concentration of inorganic carbon compounds may change in this time. Also in the recent samples pH has a tendency to increase, when measurements in the field and the laboratory are compared. Probably the figures for HCO_3^- are too high, especially in the old samples.

The chemical parameters have been divided in seven groups, depending on the degree of correlation with the first principal component (PC 1). PC 1 has a very strong positive correlation with the parameters of group 1 in Table 5 and a very strong negative one with the parameters of group 7. The parameters in these groups are very strongly intercorrelated too. PC 1 is strongly correlated with group 2 and 6, well correlated with group 3 and 5 and not correlated with group 4.

The strongest correlations are not found between PC 1 and the absolute concentrations of ions, but

Table 5. Chemical data of moorland pools and precipitation. Recent samples are in decreasing order of score on first principal component (PC1). Physico-chemical parameters are in decreasing order of correlation with PC1. r_{PC1} = Spearman rank correlation coefficient between chemical data and score on PC1 of recent samples. tr = trace, n.d. = not detectable.

				Recent samples															Old samples[a]			Precipitation[b]		
		Station number		V2	B6	B3	B4	V1	B5B	B8	B1	D6	B7	B2	D3	D4	D2	D1	D5	B6	V1	B5B	B	V	D
		Year (19..)		77	78	78	78	78	78	78	78	78	78	78	78	78	78	78	78	20	30	19	78	78	78
		Month		11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	4	4	11			
group		Score on PC1		266	251	250	242	221	218	210	173	168	138	39	-31	-43	-133	-135	-144	-137	-140	-127	-	-	
1	0.85	$SO_4^{2-}/(Cl^- + SO_4^{2-} + HCO_3^-)$		0.78	0.64	0.69	0.70	0.64	0.77	0.73	0.77	0.58	0.54	0.44	0.44	0.37	0.23	0.19	0.31	0.23	0.41	0.23	0.68	0.67	0.59
	0.79	$Ca^{2+}/(Ca^{2+} + Cl^-)$		0.46	0.44	0.39	0.45	0.34	0.53	0.48	0.44	0.25	0.35	0.29	0.19	0.10	0.11	0.25	0.16	0.22	0.29	0.23	0.27	0.34	0.28
	0.76	$Ca^{2+}/(Ca^{2+} + Mg^{2+} + Na^+ + K^+)$		0.31	0.44	0.32	0.37	0.27	0.41	0.35	0.36	0.20	0.31	0.30	0.18	0.09	0.10	0.25	0.14	-			0.32	0.29	0.24
	0.73	Ca^{2+}	meq l^{-1}	0.20	0.20	0.17	0.25	0.17	0.55	0.35	0.25	0.12	0.15	0.10	0.15	0.05	0.05	0.15	0.07	0.07	0.20	0.17	0.043	0.040	0.034
	0.72	SO_4^{2-}	meq l^{-1}	0.69	0.44	0.62	0.69	0.62	1.64	1.00	1.08	0.54	0.37	0.21	0.48	0.29	0.12	0.12	0.19	0.10	0.40	0.21	0.175	0.158	0.127
2	0.62	$Mg^{2+}/(Ca^{2+} + Mg^{2+} + Na^+ + K^+)$		0.31	0.24	0.20	0.27	0.29	0.28	0.29	0.23	0.25	0.19	0.21	0.23	0.19	0.22	0.18	0.23	-		-	0.18	0.18	0.17
	0.61	Al^{3+} [d]	mg l^{-1}	-	0.4	0.8	1.0	1.0	5.0	2.0	3.5	0.5	0.2	0.1	1.0	0.4	0.1	0.1	0.1	-		-	-	-	
	0.55	EC_{25} (field)	mS m^{-1}	-	9.5	14.8	12.9	15.4	28.5	19.7	15.2	14.3	7.4	6.3	12.8	10.1	6.5	6.4	11.4				-		
	0.53	NH_4^+-N-in./(NH_4^+-N-in. + NO_3-N)		0.88	1.00	1.00	1.00	0.91	0.99	0.75	1.00	0.96	0.71	1.00	0.66	0.98	0.83	0.57	0.78	-			-		
3	0.47	EC_{25} (lab.)	mS m^{-1}	14.3	8.6	11.6	12.7	12.7	27.5	19.3	16.7	12.7	7.9	5.7	13.8	10.2	6.9	7.6	9.8	4.6	9.7	9.7	6.4	5.7	5.3
	0.32	Mg^{2+}	meq l^{-1}	0.17	0.12	0.11	0.18	0.19	0.38	0.29	0.16	0.16	0.09	0.07	0.19	0.10	0.11	0.12	0.13	0.08	0.20	0.16	0.024	0.025	0.025
4	0.01	K^+	meq l^{-1}	0.01	0.02	0.07	0.03	0.03	0.04	0.03	0.03	0.01	0.04	0.01	0.03	0.06	0.03	0.02	0.03	-			0.004	0.005	0.005
	0	NO_3-N	µg l^{-1}	<3	<3	<3	<3	<3	<3	<3	<3	<3	<3	<3	<3	<3	<3	<3	<3	n.d.	n.d.	n.d.			
	-0.05	NH_4^+-N-inorganic	mg l^{-1}	0.23	0.04	0.66	0.14	0.70	2.9	0.47	1.17	0.47	0.27	0.23	0.39	3.7	0.70	0.12	0.18	tr.	0.30	tr.	1.7	2.0	1.3
	-0.11	HCO_3	meq l^{-1}	0	0	0	0	0	0	0	0	0	0.03	0.03	0	0.05	0	0.07	0	0.08	0.10	0.15	0	0	0
5	-0.45	PO_4^{3-}-P (ortho)	µg l^{-1}	3	7	7	3	7	7	7	3	3	20	7	3	52	10	10	7	n.d.	n.d.	n.d.	11	10	7
	-0.48	$KMnO_4$-cons. (filtr.)	mg l^{-1}	3	3	4	4	4	8	3	4	1	35	9	2	45	5	7	10	11	13	14			
	-0.49	HCO_3/($Cl^- + SO_4^{2-} + HCO_3^-$)		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.06	0.00	0.06	0.00	0.11	0.00	0.19	0.10	0.17	0.00	0.00	0.00
	-0.49	pH (lab.)		3.8	4.3	4.0	3.9	4.1	3.9	3.8	3.7	3.8	4.7	4.6	4.0	5.1	4.4	5.6	4.0	-			4.2	4.4	4.4
	-0.49	Na^+	meq l^{-1}	0.20	0.13	0.20	0.22	0.26	0.37	0.33	0.26	0.35	0.20	0.15	0.46	0.33	0.30	0.33	0.33	-			0.063	0.070	0.078
	-0.50	$KMnO_4$-cons. (unfiltr.)	mg l^{-1}	12	10	4	7	7	15	9	4	1	70	9	4	75	55	35	25	-					
6	-0.51	NO_3-N	mg l^{-1}	0.03	0.00	0.00	0.00	0.07	0.02	0.16	0.00	0.02	0.11	0.00	0.20	0.07	0.14	0.09	0.05	n.d.	n.d.	n.d.	0.8	0.9	0.8
	-0.57	Fe	mg l^{-1}	0.21	0.18	0.09	0.06	0.07	0.42	0.14	0.09	0.50	1.4	0.33	0.15	0.35	0.55	0.75	0.22	<0.1	0.15	<0.1			-
	-0.58	pH (field)		3.7	4.2	3.9	3.8	3.8	3.7	3.6	4.0	3.7	4.6	4.6	3.8	4.5	4.5	4.6	4.3	~4.5		~5.5			
	-0.62	Cl	meq l^{-1}	0.20	0.25	0.28	0.30	0.35	0.49	0.38	0.32	0.39	0.28	0.24	0.62	0.44	0.41	0.45	0.42	0.25	0.47	0.54	0.082	0.079	0.087
	-0.64	NH_4^+-N-organic	mg l^{-1}	0.31	0.02	0.14	0.16	0.14	0.14	0.27	0.16	0.27	0.54	0.16	0.16	0.74	0.58	0.43	0.31	0.28	0.18	0.22			
7	-0.77	EC_{25}/Cl : EC_{25} (field)			0.20	0.15	0.18	0.17	0.13	0.15	0.16	0.21	0.29	0.29	0.37	0.33	0.48	0.54	0.28						
	-0.82	EC_{25}/Cl : EC_{25} (lab.)		0.11	0.23	0.19	0.18	0.21	0.14	0.15	0.13	0.24	0.27	0.32	0.34	0.33	0.45	0.45	0.33	0.42	0.37	0.42	0.10	0.11	0.13
	-0.82	Cl : (Cl + SO_4^{2-} + HCO_3^-)		0.23	0.36	0.31	0.30	0.36	0.23	0.28	0.23	0.42	0.41	0.50	0.56	0.56	0.77	0.70	0.69	0.58	0.49	0.60	0.39	0.33	0.41
	-0.82	($Na^+ + K^+$)/($Ca^{2+} + Mg^{2+} + Na^+ + K^+$)		0.38	0.33	0.48	0.37	0.44	0.31	0.36	0.41	0.55	0.50	0.49	0.59	0.67	0.67	0.57	0.63				0.50	0.54	0.59
	-0.83	($Na^+ + K^+$)/($Ca^{2+} + Mg^{2+}$)		0.62	0.48	0.93	0.58	0.78	0.44	0.56	0.71	1.24	1.00	0.94	1.44	2.60	2.06	1.46	1.71				1.01	1.16	1.42
		CO2	mmol																	0.07	0.11	0.05		-	

[a] Borrowed from Redeke & de Vos (1932). Redeke (1948) and J. Heimans (pers. comm.)

[b] Yearly averages of the stations Gilze-Rijen and Eindhoven (B), Deelen (V) and Witteveen (D) taken from Anonymous (1979). The figures for B are mean values of Gilze-Rijen and Eindhoven

[c] Only recent samples have been used for calculation of r_{PC1} (no correction for ties). Significancy levels: r = 0.51: P = 0.05; r = 0.67: P = 0.01; r = 0.85: P = 0.001.

[d] All Al-species assumed to be present as Al^{3+}

between PC 1 and some ratios. $(Na^+ + K^+)/(Ca^{2+} + Mg^{2+} + Na^+ + K^+)$, $Ca^{2+}/(Ca^{2+} + Mg^{2+} + Na^+ + K^+)$ and $Mg^{2+}/(Ca^{2+} + Mg^{2+} + Na^+ + K^+)$ are the relative concentrations of $(Na^+ + K^+)$, Ca^{2+} and Mg^{2+} referred to their sum (= sum of major cations) and define the points in Fig. 21. The ratio $Ca^{2+}/(Ca^{2+} + Cl^-)$ can be used as an easy-to-measure surrogate for the relative Ca^{2+}-concentration, because the proportion of Mg^{2+} is rather constant in surface and ground waters, the proportion of K^+ is fairly small and Na^+ is highly correlated with Cl^- (Van Wirdum 1980). $(Na^+ + K^+)/(Ca^{2+} + Mg^{2+})$ is the ratio of univalent to divalent cations, which was recognized to be an important factor for the spatial distribution of algae by Pearsall (1921). It is closely related to the relative $(Na^+ + K^+)$-concentration. In the same way the relative concentrations of the anions Cl^-, SO_4^{2-} and HCO_3^- are defined. The ratio of the calculated electrical conductivity of the Cl^--ions present in the sample ($EC_{25}(Cl^-)$) and the electrical conductivity of the sample (EC_{25}) is an easy-to-measure surrogate for the relative Cl^--concentration, as the electrical conductivity is correlated very strongly with $(Cl^- + SO_4^{2-} + HCO_3^-)$ (Van Wirdum 1980). Because HCO_3^- is of minor importance or absent at all in the moorland pools, this ratio may be used as a surrogate for the relative SO_4^{2-}-concentration too.

For a first inspection of the data Spearman rank correlation coefficients have been used, because we had no *a priori* model of the relationships between environmental and species composition parameters. Product moment correlation coefficients before and after logarithmic transformation of chemical data have been calculated too. Then the most salient relationships are those between PC 1 and log $[SO_4^{2-}]$ ($r^2 = 0.69$; $P < 0.001$) and the relative concentrations of SO_4^{2-} and Cl^- (both $r^2 = 0{,}90$; $P < 0.001$). The first two relations are visualized in Fig. 22 and 23.

Other positive correlations are between PC 1 and the relative Mg^{2+}-concentration, Al^{3+}, EC_{25}, and somewhat weaker between PC 1 and organic NH_4^+-N, Cl^-, pH, Fe, NO_3^--N, Na^+, $KMnO_4$-consumption, PO_4^{3-}-P and the relative HCO_3^--concentration.

Al^{3+}, Ca^{2+} and to a lesser extent Mg^{2+} often have relative high concentrations in acidified waters, because these ions are easily leached from the soil in watersheds that are exposed to acid precipitation (Dickson 1975, 1978; Likens & Bormann 1975; Gjessing *et al.* 1976; Wright & Gjessing 1976; Almer *et al.* 1978; Cronan & Schofield 1979). The increase in concentration of these ions and of SO_4^{2-} and H^+ causes an increase of electrical conductivity. Thus PC 1 may be interpreted as an acidification component. Acidity also restrains the activity of nitrifying bacteria (Hutchinson 1957; Wetzel 1975), which may be the cause of the good correlation between PC 1 and the ratio inorganic NH_4^+-N/(inorganic NH_4^+-N + NO_3^--N).

Dystrophic and bog waters have a high $KMnO_4$-consumption and are often rich in iron, which forms complexes with humic substances (Wetzel 1975; Gjessing 1976). These waters may be also moderately rich in PO_4^{3-}-P (Wetzel 1975; Prakash *et al.* 1975), which is correlated negatively with PC 1, like $KMnO_4$-consumption and Fe. Organic NH_4^+-N and NO_3^--N are correlated negatively too with PC 1. Wetzel (1975) states the N-level to be 'moderate' for dystrophic lakes and 'low' for clear water oligotrophic lakes. Bog lakes are fed by rain water, which is relatively rich in Na^+ and Cl^- and poor in Ca^{2+}. Moreover, peatmosses exchange hydrogen ions more strongly with divalent cations than with univalent ones (Anschütz & Gessner 1954; Clymo 1967). Therefore the relative concentration of $(Na^+ + K^+)$ and the absolute concentration of Na^+ is high in dystrophic and bog waters (Wetzel 1975). Cl^-, which is like Na^+ of marine origin in precipitation, is often closely associated with Na^+ in bog waters (Tolpa & Gorham 1961). Therefore the absolute and relative Cl^--concentrations are also negatively correlated with PC 1. All variables which have a negative correlation with PC 1 are connected with ombrogenic, dystrophic waters. High humus content apparently counteracts man-made acidification.

Thus acidification causes a shift from ombrogenic to soligenic environment, which can be easily seen from the cation triangle in Fig. 21. Ombrogenic (often dystrophic) moorland pools of the Drenthian district are in the right corner, soligenic (mostly clear water) pools are in the centre of Fig. 21. Ombrogenic pools have a high proportion of chloride, soligenic pools have a high proportion of sulfate, which can also easily be seen in Fig. 21. In this Figure and in Fig. 22 and 23 also the data of

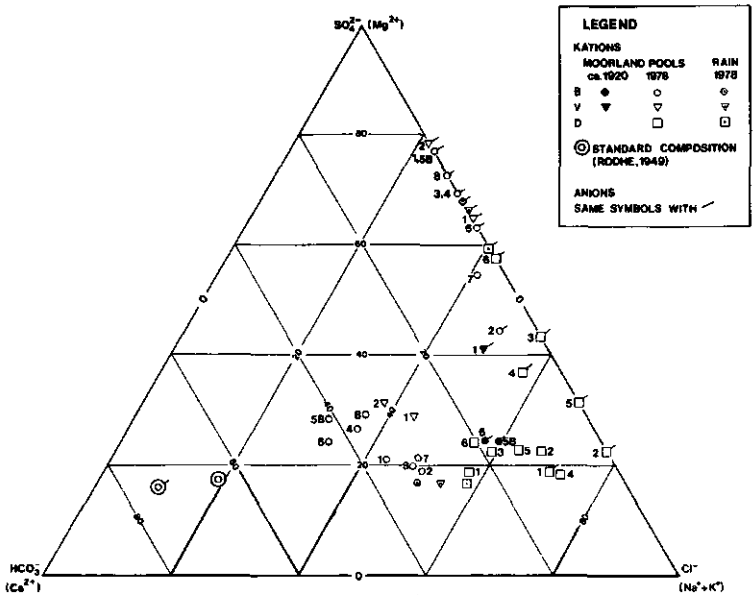


Fig. 21. Combined anion-cation triangular diagram.

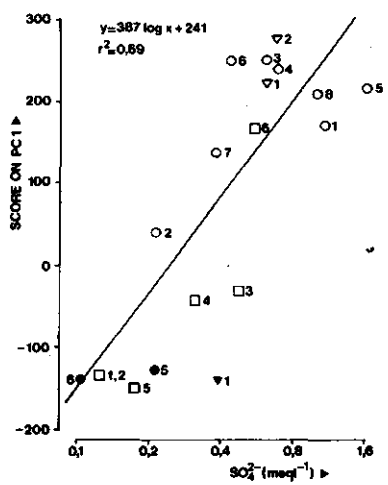


Fig. 22. Semi-logarithmic plot of absolute sulfate concentration and score on first principal component. Symbols as in Fig. 20.

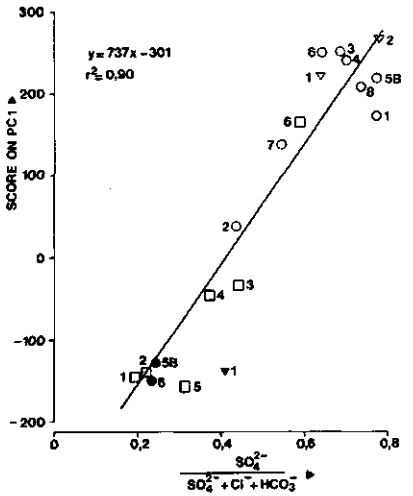


Fig. 23. Plot of relative sulfate concentration and score on first principal component. Symbols as in Fig. 20.

three old samples are plotted. The chemical and diatom samples of pools B5B and B6 were taken in about the same year. The chemical sample of V1 was taken twelve years after the diatom sample. The relative and absolute sulfate concentrations increased considerably between about 1920 and 1978, as well as the score on PC 1. The absolute chloride concentration is about the same in 1978 as in the old samples, which means that the changes in chemistry very probably are caused by increase of the sulfate concentration.

Eunotia exigua has a high loading on PC 1 (Fig. 20) and therefore has a high rank correlation ($r = 1$) with this component. The species has nearly the same correlations with chemical parameters as PC 1 and is an excellent indicator species for acidification. Especially *Frustulia rhomboides* var. *saxonica* and *E. lunaris* have high negative loadings on PC 1 and are therefore highly negatively rank correlated with this component ($r = -0.88$ and 0.79 respectively). Good development of these species is indicative for non-acidified moorland pools.

The most significant rank correlation ($r = 0.84$) between diversity indices and chemical parameters is between Δ_2 and $EC_{25}(Cl^-)/EC_{25}$(field). The rank correlation coefficient between Δ_2 and the relative sulfate concentration is 0.74. As may be expected from the projection of the origin in the PCA, the correlation between Δ_2 and PC 1 is also high ($r = -0.88$). Δ_2 and the other indices of the Hill-family decrease with increasing acidity.

PC 2 and 3 are less easy to interpret than PC 1, because chemical analyses are, with a few exceptions, only available for the recent samples which have relatively low scores on PC 2 and 3. Presumably the variation in the old samples, which have high scores on these components, is connected with small differences in chemistry, caused by regional factors (soil, hydrology) and the presence of humic substances.

The absolute and relative concentrations of rain water constituents is given in Table 5 and Fig. 21. It appears that the absolute and relative $(Na^+ + K^+)$-concentrations are increasing in the order B, V, D, which corresponds with this sequence in the water of the moorland pools. The increase of the relative $(Na^+ + K^+)$-concentration in the Drenthian pools and the decrease of this concentration in the Brabantine and Veluvian pools can be nicely seen in Fig. 21. The absolute concentration of rain water sulfate increases again in the order B, V, D; the relative concentration is highest in V and equal in B and D.

The chemistry of precipitation determines the chemical composition of moorland pool water to a considerable extent, because the sandy subsoil is extremely poor in nutrients and other soluble minerals. Also dry deposition of gases contributes to the ionic content of the water. Assuming an approximate deposition velocity of 1.1 cm s^{-1} for gaseous SO_2 on fresh water (McMahon & Denison 1979) and using the data of the national air pollution network (Anonymous 1978) the dry deposition of SO_2-S is about twice as much as the wet deposition of SO_4^{2-}-S at the nearest gauges to the moorland pools in the three areas. This can only be a very rough estimate, because the deposition velocities of SO_2 as given by various authors differ from 0.4 to 2.2 cm s^{-1} (McMahon & Denison 1979). Nevertheless the calculated ratio of wet and dry deposition is in accordance with the value that is given by Fowler (1980) for agricultural areas 30–300 km from sources. The dry deposition of particulate (aerosol) S is only a few percents of gaseous deposition (Husar *et al.* 1978).

5. Discussion

5.1 Comparison with other diatom studies

The acidification of humic poor moorland pools causes a reduction of diversity (Δ_a for $a \geq 0.25$ (section 4.3). This agrees with the hypothesis set in the introduction and the results of Berge (1976). He found a reduction of the Shannon-index, which is ln Δ_1, in diatom assemblages of some Norwegian rivers between 1949 and 1975.

By acidification the Dyer dissimilarity decreases but this is not the case with the number of species in common (section 4.4). This corresponds with the hypothesis set in our introduction and with the results of Berge (1976, 1979). This author emphasizes that acidification primarily causes quantitative changes in the diatom assemblages, while the floristic composition remains rather constant.

Acidification of humic poor pools gives rise to a huge increase of the proportion of *Eunotia exigua*, at the cost of *E. veneris*, *Fragilaria virescens*,

Frustulia rhomboides var. *saxonica*, *Navicula subtilissima*, *N. heimansii*, *Surirella arctissima*, *Tabellaria binalis*, *T. flocculosa* and *T. quadriseptata*.

No changes of diversity and dissimilarity can be detected in the humic pools in Drenthe. However, the species composition changes: *Eunotia exigua* increases at the cost of *E. veneris*, *Pinnularia appendiculata* and - to a lesser extent - *Frustulia rhomboides* var. *saxonica*. Berge (1979) found no clear changes in the diatom assemblages in a core of Högkleivvatn, a humic acid lake in southern Norway; which may indicate the buffering action of humic substances.

Berge (1976) finds a clear rise of *Eunotia exigua* with increasing acidity of rivers between 1949 and 1975, but the relative abundance does not exceed 18.5% (equivalent to 74 valves). The pH of the rivers where this species was abundant is between 4.8 and 6.1. He finds a decline of *Frustulia rhomboides*, which is ecologically very similar to its variety *saxonica*, between 1949 and 1975. According to Berge (1979) acidification promotes the growth of *Tabellaria binalis* and probably *Eunotia denticulata*, as recorded in the sediment of some Norwegian lakes. He found no clear relationship between the acidity of the lakes (recent pH 4.7–5.7) and the abundance of *E. exigua*.

Miller (1973) found an increase of *E. veneris* and *Tabellaria binalis* in the recent sediments of Stora Skarsjö, an acidifying clear water lake near the Swedish west coast. She found no significant change in the relative abundances of *Eunotia exigua* and *Frustulia rhomboides* (including varieties). The pH of this lake was 6.3 in 1947 and 4.5 in 1971.

The most striking difference between the Scandinavian and the Dutch situation is the difference in the behaviour of *Tabellaria binalis*, that increases in the northern countries, but decreases in the Netherlands. This may be connected with the pH which is now 3.7–3.8 in those moorland pools where *T. binalis* was abundant about 1920. At the above cited Scandinavian localities the pH is now between 4.5 and 5.7. Furthermore the northern localities have generally a lower electrical conductivity (<8 mS m^{-1}) than the Dutch ones (>6 mS m^{-1}). According to the literature the optimal development of this species is found in waters with pH 4.0–6.8 and low conductivity. One may speculate that *T. binalis* will disappear from Scandinavia when acidification continues.

Perhaps the same reasoning can be applied to *Eunotia denticulata* and *E. veneris*. *Frustulia rhomboides* has the same behaviour in Norway as its variety *saxonica* in the Netherlands. Also the less dominant role of *Eunotia exigua* in the northern countries may probably be ascribed to the less acidified and mineralized waters in Scandinavia, as compared with the Dutch situation.

5.2 Sulfur metabolism

As the recent sulfate concentration varies considerably from pool to pool (Table 5) this concentration can be changed by processes occurring in the moorland pools or their watershed. A model for the prediction of the sulfate concentration from dry and wet sulfur deposition requires quantitative information about hydrological, physico-chemical and biological processes in the moorland pools and their watersheds. As this information is not available, sulfur metabolism can be discussed only in general terms. In addition to acid precipitation also afforestation and drought may cause acidification and they are included in this discussion.

Differences in the water balance of the pools will be reflected in different concentrations of major ions, *e.g.* chloride, which is biologically and hydrologically conservative. Differences in retention time and rate of evaporation are reflected by the chloride concentration (Table 5). The ratio SO_4^{2-} / Cl is more suited to trace the changes of the sulfate concentration by biological and chemical processes than the absolute sulfate concentration. This ratio is closely related to the relative sulfate concentration (RSC), as the bicarbonate concentration is negligibly small (Table 5). When the RSC in a pool is equal to the RSC of incident rain this does not mean that sulfate production and consumption in this pool are in equilibrium, because the dry deposition of sulfur is about twice the wet deposition (section 4.6).

RSC is lowest in the Drenthian pools (except D6), which are generally rich in humus. Baas Becking & Nicolai (1934) investigated a small dystrophic pool, close and similar to D5. They measured very high concentrations of sulfuretted hydrogen and pointed out the importance of sulfate reduction in this type of moorland pools. Hongve

(1978) obtained strong experimental evidence for sulfate reduction taking place in sediments of dystrophic lakes in Norway.

Schindler *et al.* (1980) measured a strong increase of sulfate reduction in the hypolimnion of Experimental Lake 223 in a whole lake acidification experiment. Thus the mineralization of organic matter is intensified by the activity of sulfate reducing bacteria. Possibly the released nitrogen and phosphorus compounds will eutrophy the moorland pools. (The mechanism of eutrophication by sulfate addition to alkaline waters has been described by Ohle (1954). In this case the iron from ferriphosphate precipitates as ferrosulfide, because ferrosulfide is insoluble in neutral and alkaline waters, while phosphate is released. In contrast, ferrosulfide is soluble in acid bog waters (Baas Becking *et al.* 1960).)

No old chemical samples are available to test this hypothesis of eutrophication in brown water pools. The increase of the diatom *Eunotia exigua* might be interpreted as an increase of the trophic state. Coesel & Smit (1977) investigated the recent desmid assemblages in the Drenthian pools (except D6) and compared their results with the inventories of Beijerinck (1926) and Wartena (1954). The trophic ranges of desmids are fairly well known (Coesel, 1975). It appears that the number of mesotraphentic desmid species gradually increased during the past sixty years in D1, D2, D4 and D5. The rise is most spectacular in D5, that was the most oligotrophic moorland pool in this district sixty years ago. Typical oligo-mesotraphentic desmids disappeared from D3. This pool seems to be more oligotrophic than about 1920. The data in Table 5 suggest that the pools with an increased trophic state are fairly rich in humus (high permanganate consumption and high levels of iron, organic nitrogen and phosphorus), while D3 is relatively poor in humus and rich in sulfate. These observations support the hypothesis of eutrophication by sulfate reduction in dystrophic moorland pools.

B7, the only dystrophic pool among the Brabantine localities, has relatively low sulfate and high phosphate levels, as compared with the other pools in this district. The diatom assemblage is less affected by acidification than in most Brabantine pools (Fig. 20). Nevertheless the desmid flora of B7 greatly impoverished between 1920 and 1975 (Coesel *et al.* 1978). In Brabant the air is more severely polluted than in Drenthe, that is rather remote from urban and industrial areas. This may indicate that the buffering capacity of humic pools for acidification ends when the sulfur burden exceeds a certain level.

In some pools, notably V2, B5B and B1, the RSC is rather high. This may be caused by processes which accumulate sulfate. Many authors (*e.g.* Lillieroth 1950; Malmer 1961; Ohle 1965) emphasize that lowering of the water table by drought or drainage promotes the mineralization of organic sulfur compounds, by which sulfate is released. The year 1976 was extremely dry and very low water levels were osberved in the moorland pools. Large parts of the bottom were left dry. Also 1975 was rather dry. After 1976 the water level gradually rose again.

This process is reflected by the RSC in V1. In April 1974 the RSC was 0.66; in November of the years 1977, 1978 and 1979 RSC was respectively 0.73, 0.64 and 0.56. In V2 the RSC was 0.70 in July 1973 and 0.78 in November 1977. In B5B these values were for November 1978 and 1979 respectively 0.77 and 0.68 (data for 1973 and 1974 from Notenboom-Ram, 1976; for 1977 and 1979 Van Dam, unpublished). The high RSC levels in Table 5 are at least partially caused by the dry summer of 1976. As a consequence the abundance of *Eunotia exigua* increased between 1973 and 1977 in V2 (Fig. 20) and between 1975 and 1978 in B5 (compare with pool A1 in Van Dam & Kooyman-van Blokland 1978).

The effect of drought may be compared with that of snow melt. The snow pack accumulates sulfur that is released in the spring. In Scandinavian rivers sometimes fish killings are observed in this time of the year (Almer *et al.* 1978). In dry summers the reduced sulfur, that has been accumulated in the sediments, is released as sulfate.

Also the plantations of Scots pine around many Brabantine moorland pools may be responsible for the high RSC in this area. The heathlands and inland sand dunes were reafforested between 1840 and 1920. Afforestation enhances evapotranspiration (Noirfalise 1967) and consequently the concentration of ions in the soil solution and in ground water. Conifers are known to acidify soil and soil water because the litter is relatively poor in cations and exchanges hydrogen ions for cations (Malmer 1974; Odén 1976). Also the uptake of ammonium

nitrogen contributes to the 'biological acidification' by pine forests (Odén 1976). An increase of ammonium in rain water by air pollution will increase biological acidification.

In conifer stands throughfall is enriched with sulfate in comparison with incident rain. This is caused by leaching of sulfur from foliage and by dry deposition of gaseous and particulate sulfur species (*e.g.* Nihlgård 1970; Mayer 1974; Abrahamsen *et al.* 1977; Heinrichs & Mayer 1977; Mayer & Ulrich 1978). The dry deposition of sulfur species increases in the order bare soil, deciduous forest, coniferous forest. The filtering action of pines causes an increase of sulfate concentration in throughfall, stemflow and seepage water below the root zone.

The increased acidity promotes the leaching of metals; especially calcium and aluminium are found in high concentrations in seepage water. According to Malmer (1974) there seem to be no close connections between the acidification of lakes and rivers on the one hand and the acidification or any other changes in the soils of their watersheds on the other hand. Nevertheless Likens & Borman (1975) suppose that increased leaching of soil by acid precipitation will enrich lakes and rivers in the long run. As stated in section 4.6 enrichment with aluminium, calcium and magnesium has been found in Scandinavian and North-American waters that are affected by acid rain.

Linzon (1978) and Laaksovirta & Olkkonen (1979) found an increase of sulfur in pine needles with an increase of SO_2 in ambient air. Thus, when air pollution increases the sulfur content of the foliage, which directly falls in the moorland pools, will increase too.

Apart from V2 which is not taken into account, as this moorland pool was sampled in 1977, when the drought of 1976 had still a larger impact than in 1978, the highest RSC's are found in B1, B5B and B8. These pools have contact with the aquifer and are surrounded by more or less dense stands of Scots pine, especially B5B. B3 and B4 are surrounded by pines too, but these pools are not aquifer fed and have a lower RSC than the previous pools. The relatively low RSC for B2 is difficult to explain, because this moorland pool is situated in a depression with pines. This pool is supposed to be aquifer fed.

5.3 Metals

We found a very good correlation between the absolute and relative sulfate concentration on the one hand and the composition of the diatom assemblages on the other hand. Also other chemical parameters are highly correlated with PC 1 (Table 4). So it is very difficult to assess which factor is responsible for the spatial and temporal differences between the diatom assemblages.

It can be argued that sulfate governs the chemistry of the moorland pools. In the pools where old chemical samples are available the absolute chloride concentration remained rather constant in the last 60 years, whereas the absolute sulfate concentration increased considerably. Also other ions increased between 1920 and 1978, *e.g.* calcium, but this may be a consequence of enhanced cation leaching by rise of the acidity, caused by sulfate.

Schroeder (1939) found that sulfate below 4.2 meq l^{-1} is practically without influence on the distribution of diatoms. Stokes & Hutchinson (1975) tested the growing ability for the green algae *Chlorella vulgaris* and *Scenedesmus quadricauda* for sulfate concentrations in the range 0–5.2 meq l^{-1} in a bioassay. Growth of these algae was independent of sulfate concentration. This supports the hypothesis that the change of the diatom assemblages is not a direct consequence of increased sulfate levels.

Aluminium and heavy metals (Cd, Cu, Hg, Mn, Pb, Zn) are often found in high concentrations in acidified waters, not only by increased fallout in polluted areas, but also because their solubility increases with acidity (Dickson 1975; Stokes & Hutchinson 1975; Beamish & Van Loon 1977; Almer *et al.* 1978; Henriksen & Wright 1978). The maximal content of Al^{3+} reported from acidified lakes in Scandinavia is 0.68 mg l^{-1} at pH 4.0 (Almer *et al.* 1978). In B5B 5.0 mg l^{-1} at pH 3.7 was measured. According to Almer *et al.* (1978) a concentration of ca 0.1 mg l^{-1} is toxic to fishes. (Fishes do not naturally occur in moorland pools. In those pools where fishes have been introduced in the past, fish killings are observed, especially in the last five or ten years).

No systematic research on the impact of heavy metal pollution on many species of diatoms has been carried out, but it appears from some case studies that diatoms are sensitive to heavy metals

(Besch *et al.* 1972; Patrick 1977). *Eunotia exigua*, which takes most advantage from the acidification, is reported in literature to be very resistant to pollution with acids, aluminium and heavy metals and is often found in acid mine drainage. Probably the elevated levels of aluminium and heavy metals, caused by increased sulfate concentrations are more important for the distribution of diatoms than sulfate *per se*.

5.4 Oligotrophication or eutrophication?

Hydrogen ion concentration controls the solubility of aluminium, and consequently that of phosphate. Phosphates have a minimal solubility at pH 5-6. The solubility increases when pH becomes less than five or more than six (Stumm & Morgan 1970; Dickson 1978; Almer *et al.* 1978). Thus if pH drops from 4.5-5.0 to below 4.0, as is the case in many clear water moorland pools, more phosphorus is expected to become available for primary production.

Almer *et al.* (1978) showed that the relationship between biomass of phytoplankton and pH in 58 Swedish lakes is similar to the relationship of experimentally determined phosphorus solubility and pH, although they could not distinguish in phosphorus levels in the field, because of the overall low concentrations (less than 10 $\mu g\ l^{-1}$), just as in our clear water pools. According to Almer *et al.* (1978) it is not unlikely that the most acid lakes were actually richer in phosphorus and therefore had the largest biomasses.

Grahn *et al.* (1974), Grahn (1977) and Coesel *et al.* (1978) observed a strong increase of the biomass of *Mougeotia*, other filamentous algae and macrophytes, mainly *Sphagnum*, in lakes and moorland pools, which are exposed to acid precipitation. Because of the ion exchange capacity of peat-mosses this is interpreted by these authors as oligotrophication. On the other hand one may consider the mere increase of the biomass of the macrophytes as eutrophication.

No old and recent data about primary production of the moorland pools are available. Nevertheless we can get some idea about the change of the trophic state by using the species as trophic indicators, as has been done already in section 5.2. It appears from section 4.1 that especially eutraphentic diatom species increased from about 1920 to 1978, while oligotraphentic species decreased. No luxuriant growth of the former category can be observed, because most eutraphentic diatoms prefer circumneutral or alkaline waters. However, the acidobiontic *Eunotia exigua* can thrive in both oligotrophic and eutrophic environments.

It is a matter of experience that the adverse effects of human impact in wetland ecosystems are best observed in dry years. During dry summers in the beginning of this century elements of the alliance Nanocyperion, especially the association Cicendietum filiformis (*e.g. Cicendia filiformis, Juncus mutabilis, Peplis portula, Echinodorus ranunculoides*) occurred abundantly on the shores of pristine moorland pools (Beijerinck 1929; Goffart & Sternon 1936). In contrast, in the very dry summer of 1976 seedlings of species of the Bidention and related alliances (*e.g. Polygonum hydropiper, Lycopus europaeus, Eupatorium cannabinum*) were observed frequently (Van Dam & Kooyman-van Blokland 1978). The latter alliance requires more nutrients than the first one. During 1976 and after this year the amphiphyte *Juncus bulbosus* showed an explosive expansion in many oligotrophic moorland pools (see also Sykora, 1979). It is generally found in acid, oligotrophic waters, but it has a wide ecological amplitude as it may occur abundantly even in brackish and acid mine water (Schoof-van Pelt 1973; Sand-Jensen & Rasmussen 1978). So the autecology of *J. bulbosus* and *Eunotia exigua* is remarkably similar. *Juncus effusus*, a typical indicator of disturbance (Reichelt 1964), was still absent from the investigated moorland pools a few decennia ago, but it now forms a massive belt along the shore of some pools, notably B1 and V1. The species greatly increased after 1976 (see also Sykora 1979).

We agree with Almer *et al.* (1978) that acidification may not be interpretated as oligotrophication. They use the term 'acidotrophication'. Perhaps it is grammatically more correct to speak about 'acidi*-*trophication', analogous to acidification.

Summary

In November 1978 ten moorland pools in the province of Brabant (B), the Veluwe area (V) and six pools in the province of Drenthe (D) were sampled for chemistry and diatoms. Slides were

prepared from this material and from samples which were taken about 1920 at the same stations. 194 taxa were listed, of which 24 are more or less common. One species, *Navicula heimansii*, is new for science.

The wide range of pH between (B + V)-pools in 1920 (estimated from diatom spectra 4-6) is very narrow in 1978 (measured 3.7-4.6). Most (B + V)-pools are clear water lakes. No significant decline of the pH (ca 4.5) in most D-pools is observed, although some of them are very acid now (pH ca 3.7). Most D-pools are brown water lakes.

The diversity indices Δ_a (Hill 1973) decline significantly in the (B + V)-pools for $a \geqslant 0$. Δ_a has a tendency to increase with time in the D-pools, although this change is not significant. The number of species which two pools have in common does not change with time. The Dyer (1978) dissimilarity shows a significant decrease in the (B + V)-pools; no changes are found in the D-pools.

The first three components of the principal component analysis (PCA) explain 61, 9 and 6% of the total variance respectively. Old samples have lower scores on the first principal component (PC 1) than recent ones. Recent samples have lower scores on the second and third component than old ones. PC 1 is correlated well with $\log [SO_4^{2-}]$ ($r^2 = 0.69$) and even better with the relative sulfate concentration ($r^2 = 0.90$). Thus, the original variation, caused by regional factors is substituted by a sulfate controled variation.

PC 1 is also positively correlated with a number of other factors (Ca^{2+}, Al^{3+}, Mg^{2+} and electrical conductivity) of which is known that they increase by acid precipitation, and negatively with parameters which are characteristic for dystrophic bog waters (organic NH_4^+-N, Cl^-, Na^+, Fe, PO_4^{3-}-P, $(Na^+ + K^+)$ $(Ca^{2+} + Mg^{2+})$, $KMnO_4$-consumption).

PC 1 is nearly completely determined by *Eunotia exigua*, which is known to inhabit natural acid waters as well as acid mine waters. The species is very resistant to pollution by aluminium and heavy metals. Besides *E. exigua* some eutraphentic species increase by acidification. These are present in small quantities, because the low pH is an unfavourable environment for these generally circumneutral and alkaliphilous species. Typical oligotraphentic species (*e.g. Frustulia rhomboides* var. *saxonica*, *Tabellaria binalis*, *Eunotia denticulata*) decline with increasing acidity.

The range of sulfate concentration between the moorland pools (0.12-1.64 meq l^{-1}) is larger than would be expected from the sulfur deposition pattern in the Netherlands. In humic acid pools the sulfate concentration is low by sulfate reduction. Highest sulfate concentrations are found in moorland pools in depressions, that have been afforested with Scots pines. The high dry deposition of sulfur compounds on conifers adds to the sulfate concentration of seepage to these pools.

Another factor which may explain partially the high sulfate concentrations in 1978 is the severe drought of 1976. By drought and drainage organic sulfur species are mineralized and sulfate is released.

The oligotrophication - eutrophication controversy is discussed. We agree with Almer *et al.* (1978) that acidification does not cause oligotrophication and that aciditrophication is a more correct term to describe the process.

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Appendix

List of all species found with pH-indication class (see text p. 431) M = alpine, boreo-alpine, boreal or mountainous distribution within Europe.

acf		*Achnanthes altaica* (Poretzky) A. Cleve-Euler
alb		*A. brevipes* Agardh
cir		*A. delicatula* (Kützing) Grunow
alf	M	*A. exigua* Grunow
cir	M	*A. flexella* (Kützing) Brun
alf		*A. hungarica* Grunow
alf		*A. lanceolata* (De Brébisson) Grunow
cir		*A. linearis* (W. Smith) Grunow
cir		*A. minutissima* Kützing
cir		*A. peragalli* Brun & Heribaud
alb		*Actinoptychus undulatus* (Bailey) Ralfs
alf		*Amphipleura pellucida* Kützing
alf		*Amphora ovalis* Kützing
alf		*A. ovalis* var. *lybica* (Ehrenberg) Cleve
alf		*A. pediculus* (Kützing) Grunow
alb		*A. veneta* Kützing
		A. veneta var. *capitata* Haworth
alf	M	*Anomoeoneis exilis* (Kützing) Cleve
cir		*A. exilis* f. *lanceolata* A. Mayer
		A. intermedia Östrup (with some doubt)
acb	M	*A. serians* (De Brébisson) Cleve
acf		*A. serians* var. *brachysira* (De Brébisson) Cleve
acf		*A. serians* var. *brachysira* fo. *thermalis* (Grunow) Hustedt
alb		*A. sphaerophora* (Kützing) Pfitzer
alb		*Bacillaria paradoxa* Gmelin
alf		*Caloneis amphisbaena* (Bory) Cleve
		C. lagerstedtii (Lagerstedt) Cholnoky
alf		*Cocconeis placentula* Ehrenberg
		Coscinodiscus spec.
alf		*Cyclotella comta* (Ehrenberg) Kützing
alf		*C. meneghiniana* Kützing
cir		*C. stelligera* Cleve & Grunow
alf		*Cymatopleura solea* (De Brébisson) W. Smith
alb		*Cymatosira belgica* Grunow
cir	M	*Cymbella aequalis* W. Smith
alf		*C. aspera* (Ehrenberg) Cleve
acf	M	*C. cesatii* (Rabenhorst) Grunow
alf		*C. cistula* (Hemprich) Kirchner
acf	M	*C. gracilis* (Rabenhorst) Cleve
alf	M	*C. hebridica* (Gregory) Grunow
alf		*C. microcephala* Grunow
cir		*C. naviculiformis* Auerswald
acf		*C. perpusilla* A. Cleve
alf		*C. prostrata* (Berkeley) Cleve
alf		*C. turgida* Gregory
cir		*C. ventricosa* Agardh
alf		*Diatoma vulgare* Bory
alf		*Diploneis interrupta* (Kützing) Cleve
alb		*Epithemia sorex* Kützing
alb		*E. zebra* (Ehrenberg) Kützing
acf	M	*Eunotia alpina* (Nägeli) Hustedt
cir		*E. arcus* Ehrenberg
acf		*E. denticulata* (De Brébisson) Rabenhorst

acb *E. exigua* (De Brébisson) Rabenhorst
acf M *E. faba* (Ehrenberg) Grunow
acf *E. fallax* A. Cleve
acf *E. flexuosa* (De Brébisson) Kützing
cir *E. lunaris* (Ehrenberg) Grunow
acf *E. meisteri* Hustedt
acf M *E. monodon* var. *bidens* (Gregory) W. Smith
acf *E. pectinalis* (Dillwyn) Rabenhorst
acf *E. pectinalis* var. *minor* (Kützing) Rabenhorst
acf *E. pectinalis* var. *undulata* Ralfs
acf *E. pectinalis* var. *ventralis* (Ehrenberg) Hustedt
acf *E. polydentula* Brun
acf *E. praerupta* var. *bidens* Grunow
acf M *E. robusta* var. *diadema* (Ehrenberg) Ralfs
acf M *E. robusta* var. *tetraodon* (Ehrenberg) Ralfs
acf *E. sudetica* O. Müller
acf *E. tenella* (Grunow) Hustedt
acb? *E. tenella/exigua* complex
acf M *E. valida* Hustedt
acf M *E. veneris* (Kützing) De Toni
- *E.* spec. 351.1
alf *Fragilaria capucina* Desmazières
alf *F. construens* (Ehrenberg) Grunow
cir *F. lapponica* Grunow
alf *F. leptostauron* (Ehrenberg) Hustedt
alf *F. pinnata* Ehrenberg
alf *F. vaucheriae* (Kützing) Petersen
cir M *F. virescens* Ralfs
acf *Frustulia rhomboides* (Ehrenberg) De Toni
acb *F. rhomboides* var. *saxonica* (Rabenhorst) De Toni
alb *Gomphoneis olivaceum* (Hornemann) Dawson ex Ross & Sims
alf *Gomphonema acuminatum* Ehrenberg
alf *G. acuminatum* var. *coronatum* (Ehrenberg) W. Smith
alf *G. acuminatum* var. *trigonocephalum* (Ehrenberg) Grunow
alf *G. angustatum* (Kützing) Rabenhorst
alf *G. angustatum* var. *sarcophagus* (Grunow) Hustedt
alf *G. constrictum* Ehrenberg
cir *G. gracile* Ehrenberg
alf *G. intricatum* Kützing
cir *G. parvulum* (Kützing) Grunow
cir *G. subclavatum* Grunow
cir *Hantzschia amphioxys* (Ehrenberg) Grunow
acf M *Melosira distans* (Ehrenberg) Kützing
alf *M. varians* Agardh
alf *Meridion circulare* (Greville) Agardh
alf *Navicula accomoda* Hustedt
alf *N. atomus* (Kützing) Grunow
alf *N. avenacea* De Brébisson
acf? *N. brevissima* Hustedt (with some doubt)
alf *N. cryptocephala* Kützing
alf *N. dicephala* (Ehrenberg) W. Smith
alf *N. exilis* Kützing
acb M *Navicula festiva* (Östrup) Krasske
alf *N. gracilis* Ehrenberg
alf *N. gregaria* Donkin
acf? *N. heimansii* Van Dam & Kooyman
acb *N. hoefleri* Cholnoky
alf *N. hungarica* Grunow
alb? *N. hungarica* var. *lueneburgensis* Grunow
cir *N. integra* (W. Smith) Ralfs
acf *N. mediocris* Krasske
alf *N. minima* Grunow
alf *N. modica* Hustedt
cir *N. mutica* Kützing
alf *N. pelliculosa* Hilse
alf *N. peregrina* fo. *minor* Kolbe
alf *N. pseudohalophila* Cholnoky
cir *N. pupula* Kützing
cir *N. radiosa* Kützing
alf *N. rhynchocephala* Kützing
alf *N. seminulum* Grunow
acb M *N. subtilissima* Cleve
- *N. variostriata* Krasske (with some doubt)
alf *N. veneta* Kützing
alf *N. viridula* Kützing
- *N.* spec. 351.1
cir *Neidium affine* (Ehrenberg) Cleve
alf *Ne. affine* var. *amphirhynchus* (Ehrenberg) Cleve
acf *Ne. affine* var. *longiceps* (Gregory) Cleve
cir *Ne. iridis* (Ehrenberg) Cleve
cir *Ne. iridis* fo. *vernalis* Reichelt
acb *Ne. ladogensis* var. *densestriata* (Cleve) Foged
alf *Nitzschia acula* Hantzsch
alf *Ni. amphibia* Grunow
alf *Ni. dissipata* (Kützing) Grunow
alf *Ni. frustulum* (Kützing) Grunow
- *Ni. gandersheimiensis* Krasske
cir *Ni. gracilis* Hantzsch
alf *Ni. hantzschiana* Rabenhorst
alf *Ni. hungarica* Grunow
alf *Ni. inconspicua* Grunow
cir *Ni. intermedia* Hantzsch ex Cleve & Grunow
alf *Ni. levidensis* (W. Smith) Grunow
cir *Ni. palea* (Kützing) W. Smith
alf *Ni. paleacea* Grunow
alf *Ni. perminuta* Grunow
cir *Ni. perpusilla* (Kützing) Grunow emend. Lange-Bertalot
- *Ni. tenuis* W. Smith
cir *Ni. umbonata* (Ehrenberg) Lange-Bertalot (= *Ni. thermalis* (Ehrenberg) Auerswald)
- *Ni.* spec.
acf *Peronia heribaudii* Brun & Peragallo
acf M *Pinnularia appendiculata* (Agardh) Cleve
acf *P. biceps* Gregory
acf *P. borealis* Ehrenberg
acf *P. braunii* var. *amphicephala* (A. Mayer) Hustedt
cir *P. gibba* Ehrenberg
cir *P. microstauron* (Ehrenberg) Cleve
cir *P. microstauron* var. *brebissonii* (Kützing) Hustedt
acf *P. nobilis* Ehrenberg
acf *P. silvatica* Petersen
acf *P. streptoraphe* Cleve
acf M *P. undulata* Gregory
cir *P. viridis* (Nitzsch) Ehrenberg
- *P.* spec. 293.1
- *P.* spec. 363.1
alf *Rhoicosphenia curvata* (Kützing) Grunow

alf		*Stauroneis anceps* fo. *gracilis* (Ehrenberg) Cleve
cir		*S. kriegeri* Patrick
cir		*S. phoenicenteron* (Nitzsch) Ehrenberg
alf		*S. smithii* Grunow
-		*S.* spec.
acf	M	*Stenopterobia arctica* Cleve-Euler
acf		*S. intermedia* Lewis
alb		*Stephanodiscus astraea* (Ehrenberg) Grunow
alb		*S. dubius* (Fricke) Hustedt
alb		*S. hantzschii* Grunow
alf		*Surirella angusta* Kützing
acf	M	*S. arctissima* Schmidt
alf		*S. biseriata* De Brébisson
		S. didyma Kützing
cir		*S. linearis* W. Smith
cir		*S. linearis* var. *constricta* (Ehrenberg) Grunow
alf		*S. ovata* Kützing
alf		*Synedra pulchella* (Ralfs) Kützing
cir		*S. rumpens* Kützing
alf		*S. tabulata* (Agardh) Kützing
cir	M	*S. tenera* W. Smith
alf		*S. ulna* (Nitzsch) Ehrenberg
acb	M	*Tabellaria binalis* (Ehrenberg) Grunow
acf		*T. flocculosa* (Roth) Kützing
acb		*T. quadriseptata* Knudson

HOOFDSTUK 4

ACIDIFICATION AND ALKALIZATION OF MOORLAND POOLS IN RELATION TO WATER DEPTH AND DROUGHT

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SUMMARY

1. Relations between acidification by atmospheric deposition, morphometry and the occurrence of dry summers in this century, as well as their effects on chemistry, macrophytes and diatoms in one humic and two clearwater moorland pools are described.
2. Direct observations and biological data indicate a decrease of pH by 1-2 units in the clearwater pools and about 0.5 unit in the humic pool over six decades.
3. The drought of 1976 evoked no increase of the sulphate concentration or biological changes in the humic pool, where about 20% of the bottom surface dried up.
4. In the clearwater pools much larger proportions of the sediments desiccated in 1976 and observed concentrations of sulphate were highest in 1977-78 and decreased since then. Juncus bulbosus had a maximum in 1977-80, Eunotia exigua became the dominant diatom after 1976 and decreased since 1981 in the pool with the shortest residence time (three years).
5. In the clearwater pools the long-term decrease of pH is much larger than in softwater lakes in Scandinavia and North America. In the last fifty years the pH dropped rapidly after dry summers, because of oxidation of atmospherically derived reduced sulphur and nitrogen compounds which were stored in the sediments before. After such a drop the pH increased again, presumably by alkalinity production during sulphate reduction and denitrification.

INTRODUCTION

Several thousands of originally oligotrophic moorland pools are present in oligotrophic, non-calcareous, sandy areas of The Netherlands, Belgium, Germany, and Poland. Many of these pools have a perched water table, similar to some isolated lakes in Wisconsin and the Adirondacks (U.S.A.), which were found to be more susceptible to acid precipitation than groundwater-fed lakes in the same area (Eilers et al., 1983; Driscoll & Newton, 1985).

Chemistry and biota of the majority of these moorland pools are severely affected by acidification from atmospheric deposition. However, the extent of acidification of moorland pools in the same region can differ considerably, even if these pools are relatively remote and not directly influenced by human disturbance (e.g. Van Dam, Suurmond & Ter Braak, 1981; Vangenechten et al., 1981b; Roelofs, 1983; Van Dam & Beljaars, 1984).

One of the factors explaining the variation in acidification between moorland pools might be their depth distribution. The larger the fraction of

the bottom is that is exposed and oxidized in dry years, the more acid the pool is expected to be, because of mineralization of reduced sulphur and nitrogen compounds which are accumulated in the sediments in the years before the drought.

In this paper I will test the hypotheses that depth distribution and the occurrence of extremely dry years play a role in the acidification of moorland pools and that moorland pools are more severely acidified than lakes, due to their shallowness.

This is done by monitoring both chemical and biological parameters (diatoms, macrophytes) in these pools following the very dry summer of 1976. In addition, historical data are used to compare the effects of dry years in the past (when no accumulation of reduced sulphur and nitrogen compounds had taken place) with those in recent years (1959, 1976). Changes in diatom assemblages are used as indicators for changes of pH (Smol et al., 1986). Aquatic macrophytes were recorded because of their importance in biogeochemical processes (Wetzel, 1983) and their sensitivity to acidification (e.g. Grahn, Hultberg & Landner, 1974; Van Dam & Kooyman-van Blokland, 1978; Roelofs, 1983).

STUDY SITES

Three pools, differing in morphometry, isolated from the main aquifer by an impervious hard layer, and very small catchment areas were selected (Fig. 1) (Schimmel & Ter Hoeve, 1952; Bakker et al., 1986; N. Straathof, pers. comm.). Time series of old diatoms samples and historical documentation about chemical and biological features and human impact on the pools and their surroundings were available.

Achterste Goorven, henceforth "Goorven" is located at 51° 34' N and 5° 13' E, ca 8 m above MSL in an area of aeolian drift sands, planted with Scots pines (Pinus sylvestris L.) in 1840. Goorven has an outflow to Voorste Goorven via a culvert (Fig. 1) in a narrow dam, which was probably constructed in the second half of the nineteenth century. Before construction of the dam, a trophic gradient was present in Goorven due to the contact of its originally oligotrophic water with the mesotrophic water of Voorste Goorven (Dickman et al., in press). In order to examine the gradient three sampling stations were selected in this pool.

Gerritsfles is located at 52° 10' N and 5° 49' E, ca 40 m above MSL in an area of undeveloped soils of aeolian drift sands and podzols. Until ca 1920 the surrounding landscape was entirely open, with sand dunes bare or overgrown with grasses and podzols, mainly covered with Calluna heath (Schimmel & Mörzer Bruijns, 1952). To date the sand dunes are being invaded by Scots pines and the former heathlands are covered by Molinia caerulea (L.) Moench. Outside the catchment area, close to the northwestern shore, is a small lot of grassland, fertilized until ca 1965 (H.Schimmel, pers. comm.) and cows drank from the water of the pool (Wigman, 1932). Until 1940 sheep drank once a week at the southeastern shore of the pool (Moerman 1934; H. Schimmel, pers. comm). Nowadays roedeer and boar visit the pool regularly. Tourists occasionally bathed in the pool from about 1920 until 1965 (Wigman, 1932; A. Minnen, pers. comm.).

Kliplo is located at 52° 50' N and 6° 26' E, ca 13 m above MSL in an area similar to the previous locality. The originally open landscape of heathland and sand dunes has been invaded by Scots pines since 1920. A strip of quivering bog (5-10 m wide) separates the open water from a heathland with Juniperus communis L. at the western side of the pool, where the forest was cut in 1965. At the southeastern side the pool has a sandy beach, bordering

pine forest. For the rest Kliplo is enclosed by trees. Presumably Kliplo has been used as a drinking and washing place for sheep in the past, but no historical evidence was found. Tourists used the pool as a bathing place, at least from 1939 until 1971 (Brouwer, 1968; P. Kerssies, pers. comm.).

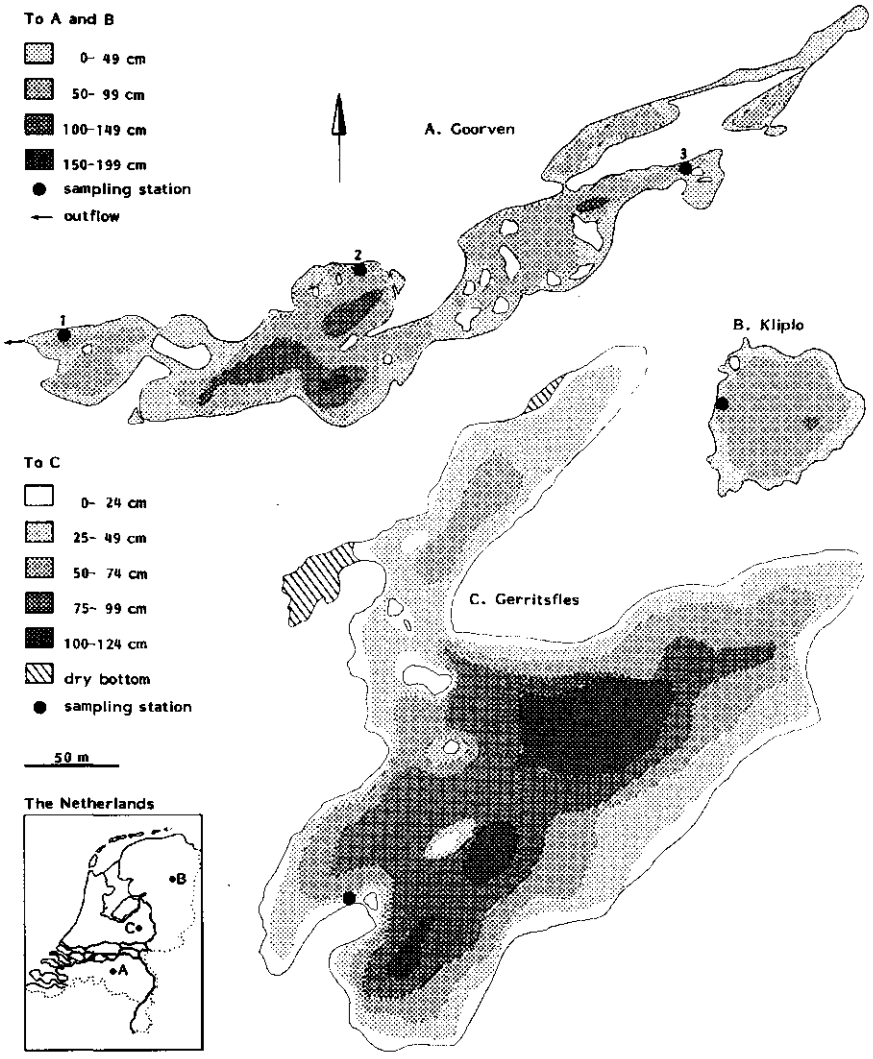

FIG. 1. Bathymetric maps (water depth in September 1984) and location of study sites in The Netherlands.

MATERIALS AND METHODS

Morphometry and hydrology

Bathymetric maps were constructed by measuring the water depth on a grid (distance 10-20 m).

Water levels of Goorven and Gerritsfles were recorded monthly from July 1979 through June 1980 and quarterly from August 1981 through February 1985. Quarterly observations in Kliplo were carried out from May 1981 through February 1985.

Chemistry

Water sampling for chemical measurements was carried out simultaneously with recordings of water level. pH was measured on the spot with a Metrohm E488 pH-meter, a WTW 91 pH-meter or a Gallenkamp pH-stick. Electrodes were calibrated with buffer solutions of pH 7 and pH 4, regularly checked with a buffer solution of pH 3 and discarded when the reading differed more than 0.1 unit from 3.0. Electrical conductivity (reference temperature 25°C) was measured with a Yellow Springs Instrument 33 or a WTW 91 conductivity meter. Water samples were collected in polyethylene bottles and stored at 4°C within 8 h after sampling.

Analysis started within 48 h after sampling. Chemical methods are described by Van Dam *et al.* (1981), except platina-colour, which was measured by comparing the extinction of the samples at = 320 nm with the extinction of a series of reference solutions at the same wavelength. Dissolved organic carbon (DOC) was measured directly in 22 samples from the study sites and some other pools, after filtration through a Sartorius 0.45 um membrane filter by IR-analysis of CO_2 evolved at 950°C by burning, catalyzed by cobalt. In these samples DOC (μ-mol l^{-1}) was found to be related to $KMnO_4$ consumption (mg l^{-1}) in unfiltered water according to: DOC = 423.1 + 13.41($KMnO_4$ consumption) (r = 0.71). Organic anions were estimated from DOC following the method of Oliver, Thurman & Malcolm (1983), where C_1 was taken as 5.5 μ-equiv. mg $^{-1}$C (Henriksen & Seip, 1980). In these C_c 22 samples bicarbonate was determined by IR-analysis of CO_2 by phosphate acid at 155°C and alkalinity by titration with 0.1 N HCl down to pH 4.4. About half of the alkalinity appeared to be caused by the presence of bicarbonate, the other half by organic anions. Where no direct measurements of DOC and bicarbonate were done, the values were estimated from $KMnO_4$ consumption and alkalinity respectively, using the relationships observed in the 22 samples.

Chemical composition of bulk precipitation was measured monthly in pooled weekly samples, collected within 100 m from Gerritsfles and Kliplo and 4 km east of Goorven from January 1982 through December 1984 according to the methods of Frantzen & Adolphs (1985). Major constituents, measured near the pools (H.F. van Dobben, pers. comm.), were generally present in similar amounts as at the nearest stations of the National Precipitation Chemistry Network at a distance of 20-30 km from the pools. Therefore data on some minor constituents (organic anions, manganese, aluminium, iron and total phosphate) were taken from these stations (Frantzen & Adolphs, 1985; A.J. Frantzen, pers. comm.).

Chemical analyses were checked by comparing anionic and cationic charges, which always agreed within five percents.

Macrophytes

Submerged macrophytes were surveyed while mapping bathymetry. Nearshore macrophytes were recorded from the shore. Nomenclature of vascular plants follows Van der Meijden et al.(1983). Species were assigned to each of the groups acidobiontic, acidophilous, circumneutral, alkaliphilous or alkalibiontic (Hustedt, 1939) using autecological information tabulated by Iversen (1929), Zólyomi (1967), Pietsch (1976, 1977, 1982), Landolt (1977), Ellenberg (1979) and personal experience.

Diatoms

Old diatom samples were found in several collections. Plankton tow diatoms were sampled twice a year in Gerritsfles and Goorven from November 1979 onwards and in Kliplo from May 1981 through May 1984.

Methods for sampling, preparing, identifying and counting were described by Van Dam et al. (1981) and Dickman et al. (in press). Nomenclatorial and taxonomical changes by Krammer & Lange-Bertalot (1985) were included. Nomenclature of Brachysira and some Eunotia species follows Hartley (1986) and Dickman et al. (in press). Optimum pH-values for the most abundant diatom taxa ($\overline{R}$) were calculated by weighted averaging (Ter Braak & Looman, 1986) from 99 samples from 97 pristine softwater lakes and pools in Western Europe with pH-values ranging from 3.3 to 7.3. The pH (pH_{wa}) for each sample of the present investigations was estimated by weighted averaging, using the R-values of each taxon (Ter Braak & Barendregt, 1986). The inferred pH (pH_{inf}) was calculated from the relationship $pH_{inf} = 1.337pH_{wa} - 1.487$ with a standard error of 0.7 unit (C.J.F. ter Braak & H. van Dam, unpublished results). Diversity indices were calculated according to Van Dam (1982).

Statistics

Statistical tests (two-tailed) were performed according to Sokal & Rohlf (1969).

RESULTS

Morphometry and hydrology

Bathymetry in September 1984 is presented in Fig. 1. Water levels were 6, 14 and 14 cm below the average water level over the period of observation in Goorven, Gerritsfles, and Kliplo respectively. Estimated morphometric data at mean water level are summarized in Table 1. Plots of water level against relative area and relative volume are given in Fig. 2.

In the extremely dry summers of 1911, 1921, 1947, 1959, and 1976, when the evaporation excess from April through August was above 0.35 m (De Bruin, 1979), water levels in Goorven, Gerritsfles and Kliplo can be estimated to be 0.7, 0.7 and 0.5 m below the average respectively (Van Gijsen & Claassen, 1978; J. Heimans, pers. comm.; P. Kerssies, pers. comm., H. Schimmel, pers. comm.; H. van Dam, unpublished data). Accordingly, about 70, 50 and 20% of the bottom surface would have been exposed to the atmosphere (Fig. 2).

A heuristic hydrological model, based on the chloride budget, may yield some insight into the interrelationships between morphometry, the quantity and composition of precipitation, and the evaporation and is necessary for the estimation of water residence times. A moorland pool with a perched water table and without visible in- or outlet is outlined in Fig. 3, where

TABLE 1. Morphometric data at mean water level.

Variable	Goorven	Gerritsfles	Kliplo
Area (ha)	2.35	6.78	0.62
Volume ($10^3 m^3$)	14.5	45.8	5.1
Maximum depth (m)	1.85	1.24	1.14
Mean depth (m)	0.62	0.68	0.82
Length of shore line ($10^3 m$)	2.1	1.8	0.31
Shore line development	4.0	2.0	1.1

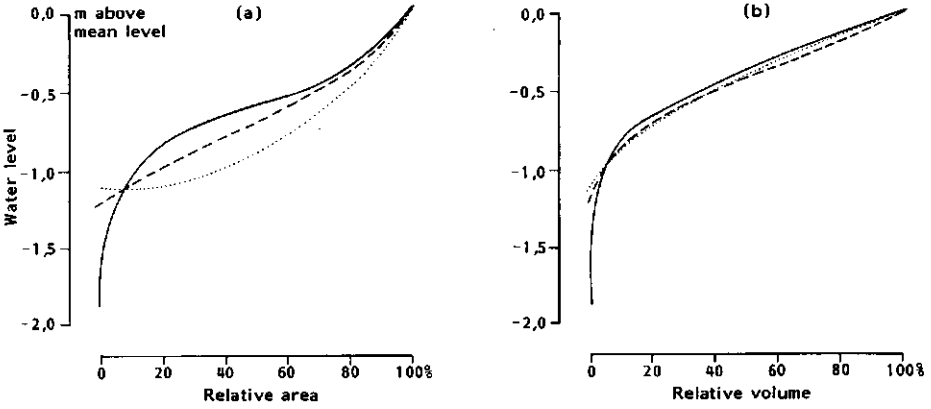

FIG. 2. Plots of water depth against relative area (a) and relative volume (b) at mean water level. Solid line: Goorven; broken line: Gerritsfles; dotted line: Kliplo.

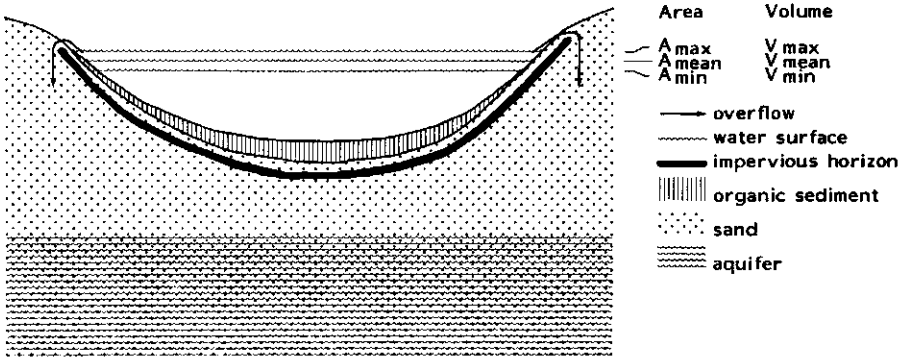

FIG. 3. Schematic cross-section of a moorland pool with minimum, mean and maximum water levels.

TABLE 2. In- and output variables of the hydrological model.

Variable	Symbol	Goorven	Gerritsfles	Kliplo
Maximum area (m^2)	A_{max}	25000	69900	6300
Minimum area (m^2)	A_{min}	22200	63800	5800
Maximum volume (m^3)	V_{max}	17170	52300	5900
Mean volume (m^3)	V_{mean}	14500	45800	5100
Annual precipitation (m)	P	0.739	0.853	0.821
Annual evaporation (m)	E	0.688	0.662	0.627
Chloride precipitation (mM)	C_p	0.069	0.084	0.090
Estimated chloride (mM)	C_e	0.47	0.33	0.35
Measured chloride (mM)	C_m	0.44	0.27	0.33
Residence time (a)	T_r	5.4	3.0	3.8

also the area of the water surface and the volume of the pool at different water levels are defined.

The annual input of chloride (F_i) can be approximated by

$$F_i = PA_{max}Cp, \quad (1)$$

where P is the annual amount of precipitation per square metre and C_p is the concentration of chloride in precipitation. A_{max} (the maximal area of the water surface) is used as a substitute for the catchment area. The annual output of chloride (F_o) can be approximated by

$$F_o = (PA_{max} - EA_{min})C_o, \quad (2)$$

where E is the annual evaporation of an open water surface per square meter and C_o is the concentration of chloride in the overflowing water. Evaporation is supposed to be most important during summer, when the water level is low. As the overflow takes place at maximum water level, C_o can be approximated by

$$C_o = C_e V_{mean}/V_{max}, \quad (3)$$

where C_e is the estimated mean chloride concentration of the surface water. In a steady state $F_i = F_o$ and combination of the expressions above gives:

$$C_e = \frac{PA_{max}}{PA_{max}-EA_{min}} \cdot \frac{V_{max}}{V_{mean}} \cdot C_p \quad (4)$$

The input and output parameters of this model, and also the calculated residence time:

$$T_r = V_{max}/(PA_{max}-EA_{min}) \quad (5)$$

are given in Table 2. V_{max} and V_{min} are the mean highest and lowest water volumes respectively in the period 1979-1985 in Goorven and Gerritsfles and 1982-1985 in Kliplo. Cm is the mean chloride concentration, which was observed in precipitation near the pools from 1982 through 1984. P and E are

average annual values from the nearest meteorological stations from 1951 to 1980 (Anonymus, 1982). The model appears to be very sensitive to changes in the evaporation, which is very difficult to estimate accurately (Table 3). In order to get comparable values the precipitation excess (P-E) is given in this table.

The differences in chloride concentrations in the pools appear to be predictable by the model at least in a semi-quantitative way, although the predicted concentrations (C_e) are systematically lower than the measured concentrations (C_m). Similarly, the residence times (T_r) are semi-quantitative estimates. In spite of the shortcomings the model explains the relatively high chloride concentration of Goorven, when compared to Gerritsfles, Kliplo, and other moorland pools (e.g. Van Dam et al., 1981).

Chemistry 1919-1985

At all four stations where pH-measurements from 1919-30 are available the pH has dropped significantly since. The median pH decreased with 2.1, 1.8, 1.2 and 0.7 units in Goorven 2, Goorven 3, Gerritsfles, and Kliplo respectively, from early values of 5.5-6 (Table 4).

Sulphate in Goorven 2 had a concentration of 0.21 mE (m-equiv. l^{-1}) in 1919 (Van Dam et al., 1981), 0.46 mE in 1975 and 0.73-1.65 mE in 1979-85. In 1919 the alkalinity was 0.15 mE, while the median alkalinity was 0.00 mE in the recent samples.

In Gerritsfles (Table 5) no changes over time were observed in the laboratory-measured pH, in contrast to the field measured pH. The alkalinity declined significantly ($P<0.01$, Wilcoxon two-sample test) between 1925-64 and 1964-68; the sulphate concentrations did not change significantly. The single measurements of ammonium in 1925 and 1930 were much lower than the median value in 1979-85, but in the most recent period values as low as in the early period occurred regularly. The chloride concentration decreased significantly ($P<0.01$, Wilcoxon two-sample test) between 1925-50 and 1960-85. This is presumably caused by the enclosure of the Zuyder Zee (now Lake IJssel), about 20 km from Gerritsfles in 1932, and the commensurate decrease in salinity which might have affected the chloride input by precipitation.

Chemistry 1974-1985

Table 6 summarizes chemical data on surface water and precipitation.

The stations Goorven 1, 2 and 3 do not differ significantly in overall water composition (Friedman's two-way analysis of variance).

Nitrite was always below the detection limit of 0.2 µE (µ-equiv. l^{-1}). Some of the variables in Table 6 have a skewed distribution and would be more properly represented by their median values, but this would hamper the calculation of ionic sums.

High concentrations of ions are associated with a growing ice-cover, while low values are found when the ice is melting. Particularly in Gerritsfles and Goorven concentrations of protons, sodium, calcium, magnesium, and chloride are lowest in the cooler and highest in the warmer seasons. Ammonium has its highest concentrations in the autumn and winter.

The precipitation chemistry near all pools (Table 6) is rather similar. Sulphate is the most important anion and is lowest near Kliplo (98 uE) and highest near Goorven (120 µE). Ammonium is the most important cation, ranging from 87 µE near Kliplo to 108 µE near Goorven. Sulphate exceeds ammonium by ca 10%.

The sites differ much more in surface water composition than in precipi-

TABLE 3. Sensitivity analysis of estimated chloride concentrations (C_e) and residence times (T_r) against difference between annual precipitation and evaporation of an open water surface (P-E).

	Goorven		Gerritsfles		Kliplo	
P-E (m)	C_e (mM)	T_r (a)	C_e (mM)	T_r (a)	C_e (mM)	T_r (a)
0.05	0.48	5.4	0.68	6.2	0.77	8.4
0.10	0.35	4.0	0.49	4.5	0.54	6.0
0.15	0.28	3.2	0.39	3.5	0.42	4.6
0.20	0.23	2.6	0.32	2.9	0.34	3.8
0.25	0.17	2.0	0.27	2.4	0.29	3.2

TABLE 4. Comparison of medians, number of observations (n) and ranges of field-measured pH values between three periods. Differences between first and third period are significant ($P < 0.05$, Wilcoxon two-sample test) at all but the first sampling station. Data from Beijerinck (1926), Redeke & De Vos (1932), Dresscher et al. (1952), Coesel, Kwakkestein & Verschoor (1978), Van Dam et al. (1981) and Van Dam (in press).

		Goorven 1	Goorven 2	Goorven 3	Gerritsfles	Kliplo
1919-30	median (n)	-	6.0 (3)	5.7 (2)	5.5 (9)	6.0 (3)
	range	-	5.5-6.6	5.4-6.0	5.5-6.5	6.0-6.5
1950-60	median (n)	5.2 (1)	-	-	4.0 (1)	5.2 (1)
	range	-	-	-	-	-
1970-84	median (n)	4.1 (18)	3.9 (20)	3.9 (19)	4.3 (18)	5.3 (34)
	range	3.3-5.0	3.3-4.9	3.4-5.6	3.9-5.5	3.9-8.8

TABLE 5. Long-term changes in median values of selected chemical variables in Gerritsfles. Data from Redeke & De Vos (1932), Dresscher et al. (1952), Van Dam et al. (1981) and Van Dam (in press).

Year	pH field	pH lab.	Alkalinity (mE)	SO_4^{2-} (mE)	NH_4^+ (mE)	Cl^- (mE)	n
1925	-	4.4	0.10	0.35	0.00	0.40	1
1928	5.5	-	-	-	-	-	1
1930	5.5[a]	-	0.10	0.40	0.02	0.47	1
1950	4.0	-	0.06	-	-	0.40	1
1960	-	4.1	0.10	0.80[b]	0.11	0.43	1
1974	3.9	4.1	0.00	0.54	0.05	0.28	1
1977	-	4.0	0.00	0.92	0.09	0.34	1
1978	4.1	4.1	0.00	0.63	0.05	0.35	1
1979-85	4.3[c]	4.5	0.01	0.27	0.09	0.25	23

a) $n = 8$; b) estimated from regression with Ca^{2+} and Mg^{2+}; c) $n = 17$

TABLE 6. Chemistry of surface water and precipitation. Mean, min. and max. denote mean, minimal and maximal values respectively in surface water (Goorven and Gerritsfles 23 quarterly measurements from August 1979 through February 1985, Kliplo 16 measurements from May 1981 through February 1985). Values in column "Rain" indicate volume-weighted mean concentration in bulk precipitation (January 1982 - December 1984).

	Goorven 3				Gerritsfles				Kliplo			
	Mean	Min.	Max.	Rain	Mean	Min.	Max.	Rain	Mean	Min.	Max.	Rain
SO_4^{2-} (μE)	620	291	1020	120	277	167	396	105	130	42	187	98
Cl^- (μE)	432	169	536	69	267	212	353	84	323	282	395	90
HCO_3^- (μE)	6	0	72	3	12	0	147	0	33	17	66	0
NO_3^- (μE)	4	0.8	10	48	8	1.6	23	50	7	0.8	19	49
$H_2PO_4^-$ (μE)	0.2	0.1	0.5	-	0.3	0.1	1.6	-	0.4	0.1	1.5	-
Organic anions (μE)	34	15	134	7	33	17	68	7	62	49	84	11
Σ Anions (μE)	1096	514	1537	247	597	460	970	246	555	478	705	248
H^+ (lab.) (μE)	92	2	314	37	33	0	99	37	4	0	16	35
NH_4^+ (μE)	173	31	416	108	99	4	261	94	41	6	94	87
K^+ (μE)	50	31	84	5	41	18	113	4	35	23	61	4
Na^+ (μE)	323	152	435	55	210	152	326	68	260	196	348	73
Mg^{2+} (μE)	143	66	239	13	67	41	107	16	69	58	91	17
Ca^{2+} (μE)	158	50	299	23	82	15	299	20	70	15	150	19
Mn^{2+}_{3+} (μE)	3	2	4	0.4	3	1	13	0.3	4	2	11	0.3
Al^{3+} (μE)	89	6	278	4	24	10	89	3	3	1	4	3
Fe^{3+} (μE)	53	12	258	6	17	1	107	5	51	18	123	5
Σ Cations (μE)	1084	478	1601	251	576	412	1116	247	537	380	669	243
Cond. (lab.) (mS m^{-1})	15.6	7.2	24.8	5.8	8.1	5.8	11.0	4.4	6.1	5.4	7.3	4.4
Alkalinity (μE)	13	0	164	6	24	0	147	0	66	33	131	0
CO_2 (μM)	386	205	886	-	154	91	432	-	163	11	432	-
Colour (mg Pt l^{-1})	13	2	43	-	9	1	22	-	30	19	43	-
$KMnO_4$-cons. (mg l^{-1})	32	4	140	-	21	3	60	-	51	30	80	-
PO_4-total (μM)	0.9	0.2	2.3	0.5	1.0	0.1	3.0	0.5	1.2	0.4	3.7	0.5
SiO_2 (μM)	31	8	112	-	9	2	22	-	10	1	30	-
H^+ (field) (μE)	151	2	314	-	64	3	198	-	10	0	39	-
Precipitation (cm a^{-1})	-	-	-	85	-	-	-	86	-	-	-	89

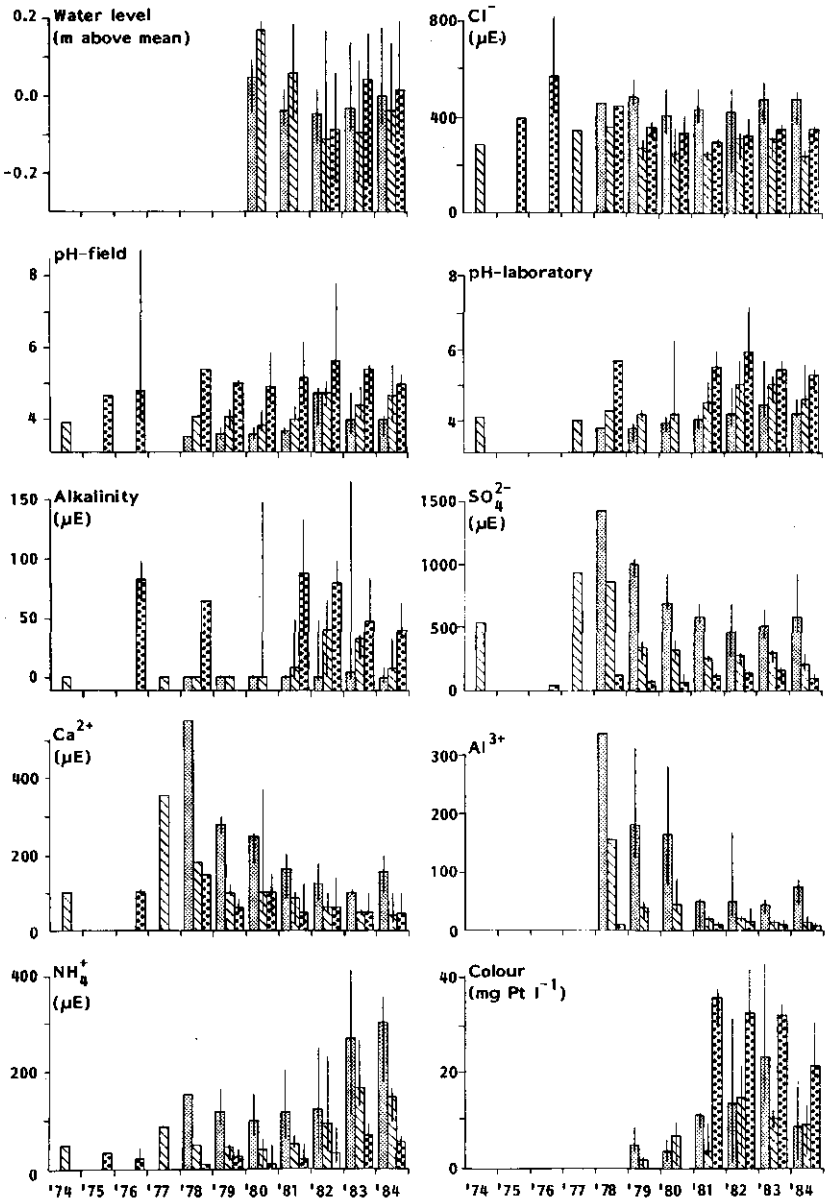

FIG. 4. Changes in median annual values (bars) and intervals (lines) of selected variables in Goorven 3 (finely dotted bars), Gerritsfles (obliquely hatched bars) and Kliplo (coarsely dotted bars) from 1974 through 1984.

TABLE 7. Trends in chemical data since 1976. r_s = 100 x Spearman-rank-correlation-coefficient of variable with time (Goorven and Gerritsfles 23 quarterly measurements from August 1979 through February 1982, Kliplo 16 measurements from May 1981 through February 1985). Significance: < 0.001 ***, P< 0.01 **, P< 0.05 *. Trends were assessed from 1979 onwards using plots as in Fig. 4. I = increase, C = constant, D = decrease, Min. = minimum, Max. = maximum, ? = trend not very clear.

	Goorven 3		Gerritsfles		Kliplo	
	r_s	Trend	r_s	Trend	r_s	Trend
Mn^{2+}	-72***	D	-72***	D	-43	D since '81
K^+	-69***	D	-17	D	-49	Max. '80, '82
Mg^{2+}	-64***	D	-85***	D	-14	C
SO_4^{2-}	-58**	D until '82	-45*	D	-22	C
Ca^{2+}	-58**	D	-68***	D until '82	10	C
Conductivity (field)	-51*	D	-9	D	38	C
Al^{3+}	-46*	D until '82	-57**	D until '81	-32	Max. '82
Conductivity(laboratory)	-42*	D	-28	D	11	C
CO_2	-40	D	-56**	D	51	I since '81
Na	-39	D	-26	D	14	C
Colour	-35	Max. '83	36	Max. '82	-65**	D
NO_3^-	-14	C	13	I?	-33	C
PO_4^{3-}-total	-3	C	-29	Max. '80-83	-76	D since '81
NO_2^-	0	C	0	C	0	C
Cl^-	8	C	-15	C	19	C
Fe	14	Max. '83	18	C	-53*	D
$H_2PO_4^-$	15	C	-31	D since '81	-69**	D since '81
SiO_2	31	I	-26	C	40	I since '81
$KMnO_4$ consumption	33	I?	16	I since '81?	-4	C
pH (field)	39	I since '82	10	I since '81	-18	C
Alkalinity	50*	I since '82	37	I since '81	-42	D since '81
NH_4^+	67***	I since '82	78***	I since '82	19	C
pH (laboratory)	77***	I since '81	42	I since '81	-39	C

tation composition (Table 6). Chloride is lowest in the pool with the shortest residence time (Gerritsfles) and highest where the residence time is longest (Goorven). Also the total concentration of ions is highest in the latter pool. Sulphate is a dominant anion only in the surface water of Goorven. In Kliplo chloride dominates, while in Gerritsfles sulphate and chloride are about equal. Nitrate is nearly absent in the pools and bicarbonate is of minor importance. Organic anions are highest in Kliplo. Sodium is the dominant cation, followed by ammonium (Goorven and Gerritsfles), and magnesium and calcium (Kliplo). Concentrations of aluminium and hydrogen-ion are high in Goorven and small in Kliplo.

Changes of water level and selected chemical variables since 1974 are shown in Fig. 4. References to observations before 1979 in Goorven and Gerritsfles and before 1981 in Kliplo are listed by Van Dam (in press). For all of the variables in Table 7, the trends since 1976 were assessed from visual inspection of similar plots as in Fig. 4. Some of the variables did not decrease or increase regularly with time, and a correlation coefficient with time by itself would give a distorted picture.

Although differing in some details the changes in Goorven and Gerritsfles have been more dramatic than in Kliplo and show a very similar pattern. Particularly in Goorven high levels of sulphate, aluminium, calcium, magnesium, sodium, potassium, and carbon dioxide were present in the first few years after the drought of 1976. Since 1978 the concentrations of these components have dropped rapidly in the few years after 1977 and more slowly after ca 1981 (Table 7). From 1981 onwards pH (field), pH (laboratory) and alkalinity increased in both pools. Colour and potassium permanganate consumption were very low during the first years after 1976, but increased after ca 1981. Ammonium increased since 1982 (Fig. 4, Table 7).

In Kliplo the chemical composition has changed little with time. The decrease in colour (Fig. 4) and other variables associated with the presence of humic substances, e.g. iron and phosphate (Wetzel, 1983), since 1981 are most striking. The pH has decreased too since 1982. Sodium and chloride (Fig. 4) peaked in the summer of 1976. However, the sulphate concentration was very low in this summer (42 µE) compared to the average concentration (130 µE). Also other parameters associated with acidification (e.g. aluminium and calcium) had low concentrations throughout the observation period.

Macrophytes

The record of 44 species of macrophytes since 1912 (Table 8) is not exhaustive, because the earlier authors (see Van Dam (in press) for references to unpublished reports and diary notes) often only mentioned the most prominent species. Nevertheless, conclusions about the decline of certain taxa are warranted.

The present vegetation of Goorven is quite uniform. In the open water Nymphaea alba is most conspicuous, although it covers only a few percents of the water surface. Juncus bulbosus and filamentous algae are increasing from station 1 to station 3. J. bulbosus covered the water surface after the severe drought of 1976 until 1979 and decreased later on. The total number of species declined from 37 in the period 1912-59 to 15 in 1984. In addition, the vegetation of the open water was much more luxuriant in the earliest period. In the early inventories $\bar{R}$ (the average pH indicator value R) ranged from 2.5 near station 1 to 1.8 near station 3. From 1974 through 1984 $\bar{R}$ was 1.6 in the whole pool. In the latter decade no clear floristic differences between the different parts of the pool could be found (Table 8).

The bottom of the open water zone in Gerritsfles is nearly completely covered with Sphagnum denticulatum Brid. (= S. crassicladum Warnst.); because of its increase over the years, places with a bare sandy bottom have nearly disappeared. J. bulbosus encroached the pool after the drought of 1976, and decreased after 1978. Prior to 1958, 20 species were recorded, whereas since 1973 only 16 species were found. $\bar{R}$ declined from 1.9 to 1.6 (Table 8).

To date the open water of Kliplo is dominated by dense stands of Potamogeton natans; its abundance increased over the last few decades, at

TABLE 8. Macrophytes of open water and nearshore areas. R is indicator value for pH (1 acidobiontic, 2 acidophilous, 3 circumneutral, 4 alkaliphilous, - indifferent). Size of symbols is proportional to abundance. Data from Thijsse (1912, 1916, 1926, 1927, 1937), Heijerinck (1924, 1926, 1931), Vuyck (1924), Bergmans (1926), Schuiling & Thijsse (1928), Koster (1942), Wigman (1932), Schimmel & Mörzer Bruijns (1952), Van Dijk & Westhoff (1960), Van der Voo (1965), Brouwer (1968), Coesel & Smit (1977), Van Gijsen & Claassen (1978), Higler (1979) and Van Dam (in press).

		Goorven					Gerritsfles		Kliplo	
	From 19..	12	12	12	75	84	16	73	24	65
	To 19..	59	59	59	76	84	58	84	58	84
R	Species Station	1	2	3	1-3	1-3				
1	Drepanocladus fluitans (Hedw.) Warnst.	·	·	·	·	·	·	·	·	·
1	Drosera intermedia Hayne		●	●	·	·			·	·
1	Drosera rotundifolia L.		●	●	·		·	·	·	·
1	Eleocharis multicaulis Sm.	●	·	●	·		·	·	·	·
1	Juncus bulbosus L.	·	·	·	●	●	·	●		·
1	Rhynchospora alba (L.) Vahl		●	●	·	·			·	·
1	Sphagnum spec.	●	●	●	●	●	●	●	●	●
2	Agrostis canina L.		·	·	·	·	●	●	●	·
2	Carex rostrata Stokes	●	●	●	●	●	●	●	●	●
2	Deschampsia setacea (Huds.) Hack.						·			
2	Eriophorum angustifolium L.	●	●	●	●	●	●	●	●	●
2	Hydrocotyle vulgaris L.	·	·		●	·	·	●	·	●
2	Hypericum elodes L.	●	●		●					
2	Juncus acutiflorus Ehrh. ex Hoffm.	·	·	·						
2	Juncus effusus L.		·		·	·	·	●	·	·
2	Lobelia dortmanna L.						·			
2	Luronium natans (L.) Raf.						·			
2	Molinia caerulea (L.) Moench	●	●	●	●	●	●	●	●	●
2	Myrica gale L.	●	●	●	●	●				
2	Potamogeton polygonifolius Pourret	●	·	·						
2	Potentilla palustris (L.) Scop.	●	·				●	·	●	●
2	Sparganium angustifolium Michx						●	·	●	·
2	Utricularia minor L.		·		·		·		●	·
2	Viola palustris L.		·				·		·	·
3	Carex lasiocarpa Ehrh.	●		·						
3	Menyanthes trifoliata L.		·						·	·
3	Myriophyllum alterniflorum D.C.	●								
3	Potamogeton natans L.	·	·	·	·		·		●	●
3	Scirpus fluitans L.		●	●			·			
3	Utricularia intermedia Hayne	●	·							
4	Alisma plantago-aquatica L.	·								
4	Eupatorium cannabinum L.	·								
4	Lycopus europaeus L.	·								·
4	Lysimachia vulgaris L.	·	·							
4	Mentha aquatica L.	·								·
4	Scirpus lacustris L.	·								
4	Typha angustifolia L.	·								
-	Eleocharis palustris L.		·				●	●		·
-	Glyceria fluitans (L.) R.Br.						●	·		
-	Juncus articulatus L.								·	·
-	Lemna minor L.							·		
-	Nuphar lutea (L.) Sm.		·		·	·				
-	Nymphaea alba L.	●	●	●	●	●				
-	Phragmites australis (Cav.) Trin. ex Steud.	●			·	·			●	●
Number of species		25	29	18	20	15	22	16	20	24
Average R		2.5	2.0	1.8	1.6	1.6	1.9	1.6	1.8	2.0

TABLE 9. Mean relative abundance of diatom taxa with a mean relative abundance of at least 1% in at least one sampling period; pH spectra, diatom-inferred pH, diversity indices of samples and optimal pH values of taxa. From 19.. to 19.. is period of sampling. + = relative abundance < 0.5% or taxon present outside the count, - = taxon not found, ' and " indicate significant (P<0.05) change in comparison to previous and next previous period respectively (Wilcoxon two-sample test).

		Goorven 1			Goorven 2			Goorven 3		Gerritsfles			Kliplo		
	From 19..	19	52	78	25	50	75	19	75	16	50	64	24	48	72
	To 19..	29	53	84	29	53	84	28	84	18	60	84	29	64	84
	Number of samples	3	2	11	5	3	12	12	12	7	5	21	2	4	11
pH-opt.	Taxon	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
4.0	Navicula subtilissima Cleve	1	1	1	1	1	+	6	+	8	1	+	8	3	17
4.1	Eunotia exigua (Brébisson) Rabenhorst	1	1	63	+	1	84	+	89	2	7	79	+	1	2
-	Navicula 'hoefleri' sensu Ross & Sims (1978)[a]	-	+	1	+	-	+	1	+	+	+	-	3	1	5
4.2	Frustulia rhomboides var. saxonica (Rabenhorst) De Toni	2	9	5	10	14	2	27	1	8	22	10	10	8	26
4.2	Navicula mediocris Krasske	+	1	1	2	1	1	+	+	1	+	-	-	+	+
4.3	Eunotia bilunaris (Ehrenberg) Mörpel	+	22	7	3	8	3	8	2	25	3	1	15	10	7
4.6	Pinnularia biceps Gregory	+	+	1	+	+	+	+	+	1	1	+	+	1	1
4.6	Tabellaria quadriseptata Knudson	+	4	3	+	9	2	15	3	1	2	5	4	1	1
4.8	Brachysira brebissonii Ross	-	1	3	2	5	1	+	1	+	+	-	-	-	+
-	B. brebissonii f. thermalis Ross	+	1	+	+	-	+	+	+	+	+	-	-	-	-
4.9	Eunotia rhomboidea Hustedt (asymmetrical forms)	+	14	3	1	4	4	+	3	7	28	3	4	3	15
4.9	Pinnularia irrorata (Grunow) Hustedt	-	1	+	-	-	-	-	-	+	+	-	-	-	-
5.0	Eunotia incisa Ehrenberg	1	22	1	2	27	1	18	+	26	9	1	16	9	6
5.0	E. rhomboidea Hustedt (symmetrical forms)	+	+	+	+	-	+	+	+	6	7	1	1	1	1
5.0	Pinnularia microstauron (Ehrenberg) Cleve	-	+	+	+	+	+	-	+	1	4	1	-	+	+
5.0	Tabellaria flocculosa (Roth) Kützing	+	1	+	2	1	+	1	+	3	3	+	24	9	6
5.2	Stauroneis anceps f. gracilis Rabenhorst	+	+	-	+	+	+	+	-	1	+	+	+	1	+
-	Eunotia elegans Østrup	+	2	1	2	1	+	1	-	+	-	-	-	-	-
5.6	Fragilaria virescens Ralfs	2	2	6	21	13	2	1	+	+	1	+	+	3	1
-	Eunotia pectinalis var. minor (Kützing) Rabenhorst	+	2	+	+	+	+	-	-	+	-	-	+	+	-
-	E. pect. var. minor f. impressa (Ehrenberg) Hustedt	1	+	+	1	-	+	+	-	+	-	-	-	-	-
5.9	Brachysira vitrea f. lanceolata (Mayer) Van Dam	17	2	2	11	6	1	4	+	5	1	+	1	26	3
5.9	Navicula leptostriata E.G. Jörgensen	1	1	+	21	2	+	17	+	1	+	-	11	14	7
-	Pinnularia appendiculata (Agardh) Cleve	-	1	-	+	-	-	+	-	3	+	+	+	-	+
-	Peronia fibula (Brébisson & Arnott) Ross	+	1	+	1	1	+	1	+	-	+	-	-	-	-
-	Cymbella rabenhorstii Ross	3	1	1	2	1	+	+	-	+	+	-	1	2	+
-	Hitzschia gracilis Hantzsch	+	1	+	1	1	+	+	+	+	-	+	+	6	1
-	N. perminuta Grunow	3	+	2	15	1	+	1	+	+	+	+	-	-	+
-	Cymbella microcephala Grunow	34	1	1	1	1	+	+	-	-	-	-	-	-	-
6.8	Achnanthes minutissima Kützing	33	6	1	1	1	+	+	+	1	1	+	2	1	+
-	Brachysira vitrea (Grunow) Ross	2	+	+	1	1	+	+	-	-	-	-	+	+	+
	Median diatom-inferred pH	6.8	5.0	4.3"	5.8	5.1'	4.1'"	4.7	4.0'	4.8	4.7	4.1'"	5.0	5.6	4.6'
	Minimal diatom-inferred pH	6.8	4.8	4.0	5.7	4.8	4.0	4.4	4.0	4.3	4.6	4.0	4.8	4.9	4.2
	Maximal diatom-inferred pH	7.2	5.1	4.8	5.9	5.3	4.5	5.8	4.5	5.0	4.9	4.4	5.2	6.1	5.1
	Median total number of taxa	36	48	34'	63	25'	29"	16	13'	22	24	12'"	31	27	25'
	Median number of taxa in count	15	31	21	23	24	16'"	10	7'	17	17	7'"	16	20	15
	Median dominance	46	35	64"	30	32	89'"	30	97'	27	35	89'"	27	27	34

[a] Not identical to the type of N. hoefleri Cholnoky (H. Lange-Bertalot & E.Y. Haworth, pers. comm.).

[b] Synonym: N. heimansii Van Dam & Kooyman.

the cost of Sparganium angustifolium. The number of species and $\bar{R}$ have increased slightly over 60 years (Table 8).

Diatoms

The 31 most common taxa are listed in Table 9, in the order of increasing pH optima. Taxa for which no optimum pH values could be calculated from my own observations are entered in their most probable place, using data from the literature as listed by Van Dam & Kooyman-van Blokland (1978) and Van Dam et al. (1981).

The diatom-inferred pH significantly decreased over time at all stations (Table 9). Between 1919 and 1929, a pH gradient existed from station 1 to 3 in Goorven; the pH encompassing a range of 2.1 units. Between 1975 and 1984, the gradient had narrowed to a range of only 1.3 units.

The most striking change over time is the huge increase of the acidobiontic Eunotia exigua in Goorven and Gerritsfles (Table 9). The majority of the taxa with higher pH-optima has decreased over time. In Kliplo a small increase of the acidobiontic Frustulia rhomboides var. saxonica has been observed. The acidobiontic Navicula subtilissima has decreased in Goorven 3 (mineral acids) and has increased in Kliplo (organic acids).

The impact of the extremely dry summers of 1921 and 1976 on the most common acidobiontic diatoms of Goorven station 3 can be read from Fig. 5.

Their median abundance decreased significantly (P = 0.05, Wilcoxon two-sample test) from 68% in 1919-21 to 45% in 1922-28. The median diatom inferred pH increased not significantly (Wilcoxon two-sample test) from 4.7 before to 5.0 after the drought of 1921. The high abundance of E. exigua in 1975, as compared with the old samples, is striking. After 1976 it dominates the assemblage with a median relative abundance of 98%. Only in the last few samples its relative abundance decreased slightly, in favour of E. bilunaris, which has a wide pH amplitude.

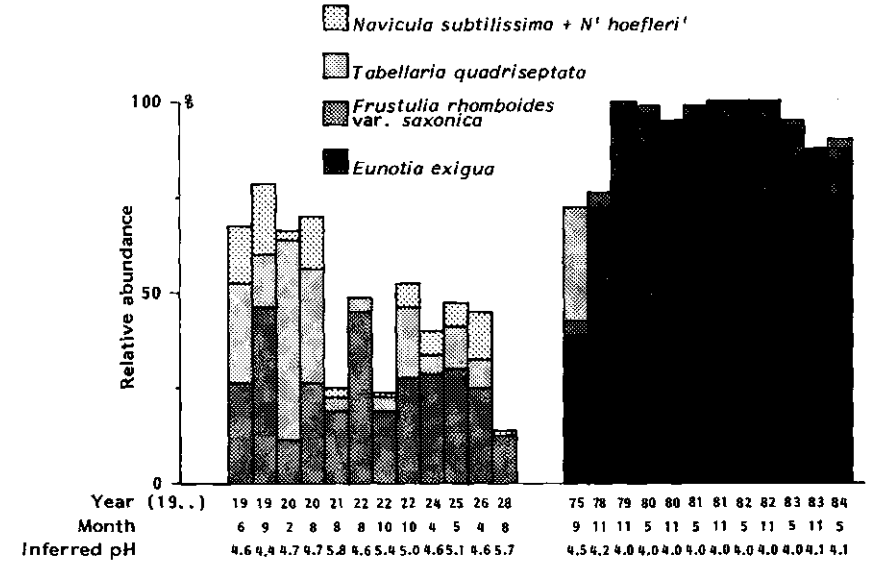

FIG. 5. Relative abundance of acidobiontic diatoms and diatom-inferred pH of Goorven 3 from 1919 through 1984.

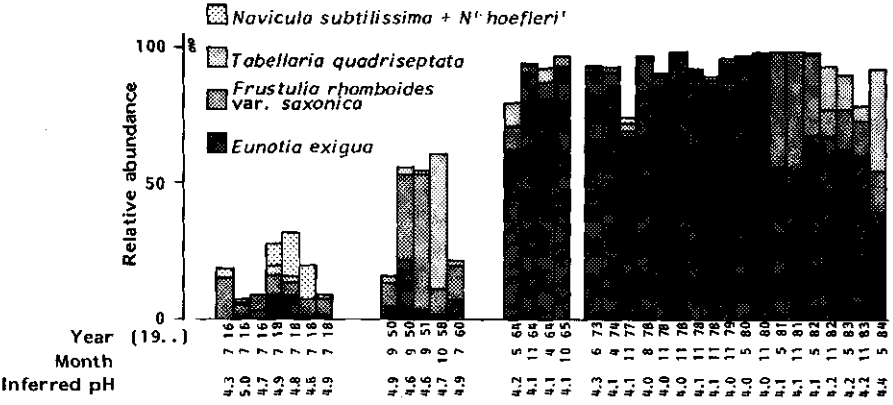

FIG. 6. Relative abundance of acidobiontic diatoms and diatom-inferred pH of Gerritsfles from 1916 through 1984.

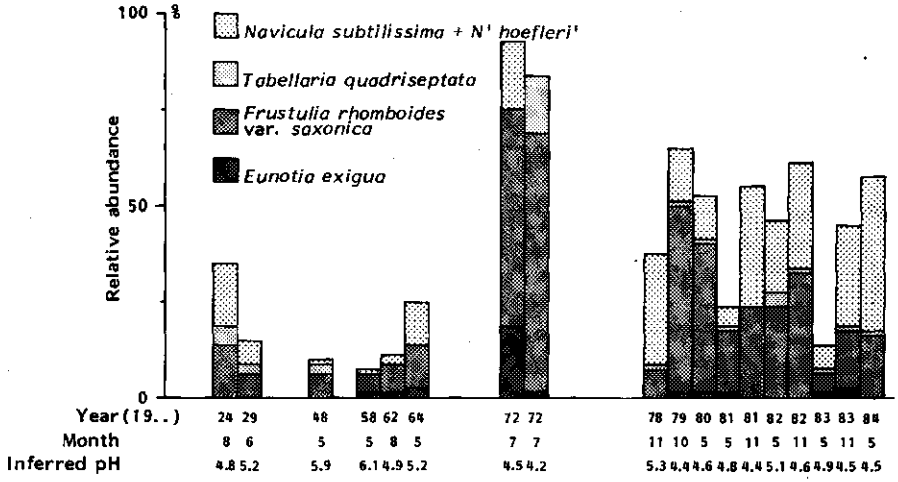

FIG. 7. Relative abundance of acidobiontic diatoms and diatom-inferred pH of Kliplo from 1924 through 1984.

In Gerritsfles acidobiontic diatoms increased after the extremely dry year 1959 with some delay. In 1964-65 their relative abundance, notably E. exigua, was over 90% and kept dominating since. From 1981 onwards E. exigua decreased. The samples from 1916, 1918, 1950 and 1978 (Fig. 6) were taken at different stations in the pool. In earlier years the spatial variation of the diatom assemblages in the pool was much larger than in 1978 (Fig. 6).

Although the acidobiontics in Kliplo in 1962 and 1964 are slightly more abundant than in 1958, no pronounced differences are seen in the diatom-inferred pH before (5.5) and after (5.3) the drought of 1959 (Fig. 7). No systematic change in either the relative abundance of the acidobiontic diatoms or the inferred pH occurs from 1978 to 1984. The extremely high abundance of the 'humic-acid diatom' Frustulia rhomboides var. saxonica in the two samples which were taken at two different places in 1972 is difficult to understand.

DISCUSSION

Long-term changes

The pH values decreased significantly over the last six decades (Table 4). Colorimetric methods, used prior to 1961, can give errors of about one pH unit in weakly buffered low alkalinity waters (Haines et al., 1983; Blakar & Digernes, 1984). The more recent potentiometric pH-measurements in these waters can give errors of about 0.7 pH unit (Neal & Thomas, 1985; Covington, Whalley & Davison, 1985). Laboratory pH-measurements could be checked by means of the charge balances. Such a check was not possible for the field-pH measurements of which the median was 0.3 unit lower than the laboratory measurements ($P<0.001$, Wilcoxon signed-rank test). The methodological problems may affect the absolute values of long-term pH changes, but

the trends are correct, as is evident from the changes in diatom-inferred pH values (Table 9) and average R values for the macrophytes (Table 8). The discrepancy between the measured and diatom-inferred pH values (Tables 4 and 9) may partly be caused by the relatively large methodological standard error (0.7 unit) of the latter value. The method of Renberg & Hellberg (1982) has a standard error of 0.3 unit in lakes with pH>4.5 (Battarbee, 1984; Charles & Norton, 1986), but requires the presence of either circumneutral, alkaliphilous or alkalibiontic taxa, which were absent from many of my samples.

The long-term pH changes as assessed by the various methods are ca 2 unit in Goorven, ca 1 unit in Gerritsfles and ca 0.5 unit in Kliplo (Tables 4, 8, 9) and far beyond the median pH decrease of 0.3 unit over the last century inferred from cores taken from 34 lakes in Scandinavia and North America (Battarbee, 1984). Thus long-term pH changes are much larger in moorland pools than in lakes and largest in those pools where the largest fraction of the bottom is exposed to the atmosphere in dry years.

The chemical composition of the moorland pool water (Table 6) is highly affected by acidification and similar to that from nearby Belgian moorland pools, discussed extensively by Vangenechten (1980) and Vangenechten et al. (1981b).

Changes in macrophyte assemblages are, again, largest in Goorven and smallest in Kliplo. The decline of isoetids (e.g. Lobelia dortmanna) and other species of low alkalinity waters (Luronium natans, Myriophyllum alterniflorum etc.) and the strong increases of Sphagnum and Juncus bulbosus are typical for acidifying lakes (e.g. Grahn et al., 1974; Van Dam & Kooyman-van Blokland, 1978; Nilssen, 1980; Roelofs, 1983; Melzer & Rothmeyer, 1983).

Long-term changes in species composition of the diatom assemblages were compared with those of other acidified areas by Van Dam et al. (1981) and Dickman et al. (in press).

Composition of precipitation

Table 10 summarizes the concentrations of some ions in precipitation at some sites in Europe and North America. Gerritsfles, Grane Langsø and Silberborn have the highest concentrations of ammonium, nitrate and sulphate

TABLE 10. Selected characters of precipitation in Europe and North America.

Site	Altitude (m)	Precip. (cm a^{-1})	H^+ (µE)	NH_4^+ (µE)	NO_3^- (µE)	SO_4^{2-} (µE)	Period	Source[a]
Birr, Central Ireland	70	78	1	11	4	14	1966-75	1
Jergul, Northern Norway	255	33	31	8	9	35	1977-79	2
Hubbard Brook, New Hampshire, U.S.A.	550	134	69	11	24	54	1963-82	3
Woods Lake, Adirondack Mts, U.S.A.	606	127	60	19	33	57	1978-81	4
Rotenfels, Black Forest, Germany	707	117	46	39	42	66	1982-85	5
Birkenes, Southern Norway	190	147	69	42	41	77	1977-79	2
Hilversum, Central Netherlands	10	71	1?	43	2	92	1933-37	6
Gerritsfles, Central Netherlands	40	86	37	94	50	105	1982-84	7
Grane Langsø, Jutland, Denmark	74	96	47	61	46	114	1977-79	8
Silberborn, Solling Mts, Germany	500	94	87	83	54	158	1969-76	9

[a] 1 Matthews & McCaffrey (1977); 2 Overrein, Seip & Tollan (1980); 3 Likens et al. (1984); 4 Johannes, Altwicker & Clesceri (1985); 5 Evers (1986); 6 Leeflang (1938); 7 Table 6; 8 Rebsdorf (1983); 9 Ulrich, Mayer & Khanna (1979).

and are situated in a belt, running from The Netherlands and Belgium to Poland, characterized by extreme air pollution (EMEP-CCC, 1984). Concentrations of sulphur dioxide in air range from 2-4 $\mu g\ m^{-3}$ at the cleanest stations (top of Table 10) to 20-30 $\mu g\ m^{-3}$ at the most polluted stations (bottom of Table 10) (EMEP-CCC, 1984). The sulphate concentration in the precipitation near Hilversum in 1933-37 is about the same as the concentration near our three study sites in 1982-84. However, the concentration of inorganic nitrogen in the earlier samples (45 μE) is much lower than in the present samples (136-156 μE). The present composition of precipitation at Hilversum is similar to that at our sampling stations (Frantzen & Adolphs, 1985).

The precipitation near the moorland pools in The Netherlands and the lakes in Jutland (5-10 m deep) is very similar (Table 10). The median diatom inferred pH (calculated according to Renberg & Hellberg (1982)) in five of these Danish lakes declined from 6.0 in ca 1945 to 5.7 in 1982 (P=0.06, Wilcoxon signed-rank test) (H. van Dam, unpublished data). The more severe acidification in the moorland pools than in the lakes might be due to a higher dry deposition of sulphur and nitrogen compounds (EMEP-CCC, 1984) and to morphometric factors.

Morphometry and hydrology

Despite the limited monitoring and hydrological data the order of magnitude of chloride concentrations is predicted correctly by the simple hydrological model (Table 2). This indicates that the input variables are the principal factors affecting chemistry, and consequently biology, of moorland pools. Differences in land use around these pools (forest, heath) are probably less important.

The residence time (T_r) gives an impression of the time needed for recovery of a lake or pool after perturbation, such as a severe drought. The estimated residence times (Table 2) are between 3 and 6 years. T_r for 57 lakes in Central Europe (median area 680 ha, median average depth 36 m), as tabulated by Siebeck (1982), is between 0.1 and 21 years (median 1.6). Residence times of acidifying lakes in North America are 0.06-25 years (Dillon, Jeffries & Schneider, 1982; Cook & Schindler, 1983; Francis, Quinby & Hendrey, 1984; Kelly et al. in press). All these lakes have in- and outlets, in contrast to most moorland pools, which may explain why moorland pools have relatively high T_r values, in spite of their small volume.

Earlier drought periods

Extremely dry years have an evaporation excess exceeding 0.35 m from April through August and occurred since 1735 about once in fifteen years, as estimated from the data by Vanderlinden (1924), Labrijn (1945) and De Bruin (1979).

Acidification of drainage water of peatlands after drought or artificial drainage is well-known (e.g. Malmer, 1974; Gorham, Bayley & Schindler, 1984). After a dry summer Högbom (1922) observed precipitation of humic substances and mass death of fish in Swedish lakes in a region with sediments rich in pyrite.

After the drought of 1921 the production of alkalinity by sulphate reduction in Goorven 3 apparently exceeded consumption of alkalinity by nitrification and subsequent denitrification (see next section). The impact of the drought period of 1921 was lower than in 1976, probably because less sulphur had been accumulated in the sediments in 1921 than in 1976. Because

TABLE 11. Comparison between actual and hypothetical mean concentration of selected ions in surface water.

	Goorven 3		Gerritsfles		Kliplo	
	act.	hypoth.	act.	hypoth.	act.	hypoth.
SO_4^{2-} (μE)	620	751	227	334	130	352
NO_3^- (μE)	4	301	8	159	7	176
NH_4^+ (μE)	173	676	99	299	41	312
H^+ (μE)	92	232	33	118	4	126
Al^{3+} (μE)	89	25	24	10	3	11

the median abundance of Frustulia rhomboides var. saxonica, an indicator of humic acids, did not change after the drought of 1921, the concentration of humic substances in Goorven 3 probably was not affected by this drought.

The dramatic increase of both sulphate (Table 5) and Eunotia exigua (Fig. 6) in Gerritsfles after the drought of 1959 indicates that the effect of this dry year was similar to that of 1976.

Drought of 1976

Expected chemistry. If a moorland pool would be an unreactive reservoir and ions would be supplied by precipitation and concentrated by evaporation only, the concentration of any ion in the reservoir (S_r) could be estimated from its concentration in precipitation (S_p), the concentration of the inert chloride ion in precipitation (C_p), and in the reservoir (C_r) by: $S_r = C_r S_p / C_p$. These hypothetical concentrations were calculated from Table 6 for some ions which are important intermediates in processes consuming and generating alkalinity (Table 11). In all pools, particularly Kliplo, the actual sulphate concentration is much lower than the hypothetical concentration. Because dry deposition of sulphurdioxide sulphur, which is about twice the wet deposition of sulphate-sulphur on moorland pools in The Netherlands (Van Dam et al., 1981), has not been considered this discrepancy is even higher than suggested in Table 11. Less than 25% of the wet deposition of inorganic nitrogen (nitrate plus ammonium) is recovered in the pools. Dry deposition of ammonium, which is probably in the same order of magnitude as the wet deposition, does decrease the recovery, so considerable amounts of inorganic nitrogen must have been removed. Protons have also lower concentrations than expected.

Sulphur. Sulphate reduction could be responsible for the relatively low sulphate concentrations. Epilimnetic sulphate reduction has been found as a major source of alkalinity in acid-sensitive Canadian lakes (Kelly & Rudd, 1984; Cook et al., 1986; Schindler et al., 1986) and considerable activity of sulphate reducers has been observed in peat bogs at pH<4 (Baas Becking & Nicolai, 1934; Hemond, 1980).

In Kliplo changes from 1974 through 1984 have been relatively small (Table 7, Fig. 4). The bottom sediment was not aerated in 1976 and the reduction of sulphate probably takes place continuously. The sulphate concentration in the interstitial water of the sediments is appreciably lower than in the open water (J. Mulder, pers. comm.). The pool is permanently stained brown. No reduced levels of humic and fulvic acids,

characteristic for acidifying lakes (e.g. Almer et al., 1978; Dillon, Yan & Harvey, 1984) occur, because in this pool no strong acids are formed by oxidation of reduced sulphur and nitrogen compounds.

In Gerritsfles and particularly in Goorven large fractions of the bottom were exposed to the atmosphere during the drought of 1976. Oxidation of reduced sulphur compounds, accumulated in the bottom sediments because of the high sulphur load in the preceding decades, caused high sulphate concentrations during refilling, as was observed in Belgian moorland pools by Vangenechten, Bosmans & Deckers (1981a). Subsequently, sulphate reduction could contribute to the decrease of sulphate concentration and increase of alkalinity. Indeed alkalinity and pH are positively correlated with time in these pools (Table 7, Fig. 4).

Kelly et al. (in press) found a positive relationship between sulphate (and nitrate) removal and water residence time, contrarily to our observations. Probably an eventual increase in neutralization due to the longer residence time of Goorven was counteracted by the higher production of protons in this pool during aeration of the sediments in 1976, when compared to Gerritsfles and, especially, Kliplo.

Sulphate reduction (and also denitrification) require the presence of organic material as electron donors. Until three decades ago many moorland pools in The Netherlands had a bare sandy bottom (e.g. Redeke & De Vos, 1930). A layer of organic detritus has developed since, due to impaired decomposition of organic material at pH values below 5 (Grahn et al., 1974; Francis et al., 1984; Rao, Jurkovic & Nriagu, 1984; Kelly et al., 1984). The increase of colour since ca 1981 might reflect increased decomposition at rising pH levels (Fig. 4).

Schindler (1985) expresses solicitude about depletion of iron in sediments of lakes when sulphate reduction will continue at accelerated rates. In that case hydrogen sulphide is no longer fixated as iron sulphides and will intoxicate the system. The continuous removal of iron might uncouple the phosphate and iron cycles, having a fertilizing effect by allowing more phosphorus to remain in solution (Ohle, 1954; Stumm & Baccini, 1978; Schindler, 1985). The increase of Potamogeton natans (more typically found in eutrophic waters) and the decrease of Sparganium angustifolium (characteristic for oligo-mesotrophic waters) in Kliplo might be signals for the enhanced availability of phosphorus in this pool. Also the changes in desmid assemblages indicate eutrophication of Kliplo since about 1925 (Coesel & Smit, 1977).

Nitrogen and carbon. Removal of atmospherically derived nitrogen by nitrification of ammonium and subsequent denitrification may explain the differences between hypothetical and actual concentrations in Table 11. Like sulphate reduction, these processes are stimulated by neutral or alkaline conditions, but also in very acid environments (pH<4) nitrification and denitrification have been reported (Keeney, 1973; Focht & Verstraete, 1977; Van Breemen et al., 1982; Hemond, 1983; Schindler, 1985). As nitrification of one mole of ammonium produces two moles of protons, while denitrification of one mole of nitrate consumes one mole of protons, the chain of reactions causes the production of one mole of protons or an equivalent consumption of alkalinity. As ammonium and sulphate are present in about equivalent amounts in precipitation, the production of protons by ammonium removal equals the consumption of protons by sulphate reduction, at least in the long run, provided that enough organic material is present. Denitrification of the nitrate nitrogen, added by precipitation, will cause an extra consumption of protons.

Carbon dioxide concentrations in Gerritsfles and particularly Goorven

were elevated during the first years after the drought of 1976 as a consequence of intensive sulphate reduction and might have been responsible for the lush growth of Juncus bulbosus in the first post-drought years (Roelofs, Schuurkes & Smits, 1984; Wetzel, Brammer & Forsberg, 1984). J. bulbosus and Sphagnum cuspidatum Ehrh. ex Hoffm. have a positive photosynthetic response with concentrations of ammonium above 50 uE (Roelofs et al., 1984). J. bulbosus and Sphagnum flexuosum Dozy et Molk. preferred ammonium above nitrate and seriously affected the ammonium concentrations in the experiments of Schuurkes, Kok & Den Hartog (1986). So the increase of ammonium in both pools since ca 1982 may have been associated with the decline of J. bulbosus since then. Also decomposition of dead J. bulbosus may play a role. In Goorven, where the biomass density of aquatic macrophytes is lowest, the ammonium concentration is higher than elsewhere. The low concentrations of inorganic nitrogen in Kliplo may be due to the lush growth of Potamogeton natans.

Cations. The cations aluminium, calcium, magnesium, sodium, and potassium have a similar pattern through time as sulphate (Table 8) and are known to be weathered at increasing rates from catchments exposed to acidification (Schnoor & Stumm, 1985) and released from sediments of acidifying lakes by cation exchange (Oliver & Kelso, 1983; Baker et al., 1985). Vangenechten et al. (1981a) observed a similar pattern in the changes of major ion chemistry in Belgian moorland pools after the drought of 1976.

Other pools and lakes. The developments in Goorven and Gerritsfles in the last decade are probably representative for other moorland pools in The Netherlands. Kersten (1985) presents the results of chemical samplings from 15 pools in 1982-85, which were sampled in 1978 by Van Dam et al. (1981). A t-test indicates significant increases of pH ($P<0.01$) and ammonium ($P<0.05$) and decrease of sulphate ($P<0.01$) in these pools, while the increase of alkalinity is not significant.

Forsberg, Morling & Wetzel (1985) observed an increase of pH and a decrease of sulphate from 1977 through 1982 in small and deep lakes in southern Sweden, which were acidified in the period before. The authors attribute the recovery of the lakes to decreased of sulphate concentrations in precipitation of ca 2% per year, which is similar to data from The Netherlands (Kempen et al., 1986). An alternative explanation would be an acid 'surge' after drainage of the soils in the watershed during the drought of 1976, followed by similar processes as were described above.

CONCLUSIONS

The long-term developments in the investigated moorland pools and some other moorland pools in The Netherlands (Van Dam et al., 1981; Van Dam, in press) are summarized and compared with long-term changes in North American and Scandinavian lakes in Fig. 8. Generally, acidification of the lakes started about 1930 and the pH decreased by about 0.3 unit (Battarbee, 1984; Charles & Norton, 1986).

Acidification of moorland pools in The Netherlands started several decades earlier, because they are closer to major sources of atmospheric pollution. Particularly in those pools where a large part of the bottom desiccates during drought episodes, the long-term decrease of pH is much larger than in lakes. During the last fifty years the pH dropped rapidly after dry summers, because of oxidation of atmosphere derived reduced sulphur and nitrogen compounds, which had been stored in the sediments. After such a drop the pH increased again, presumably by alkalinity production during sulphate reduction and denitrification. This process probably

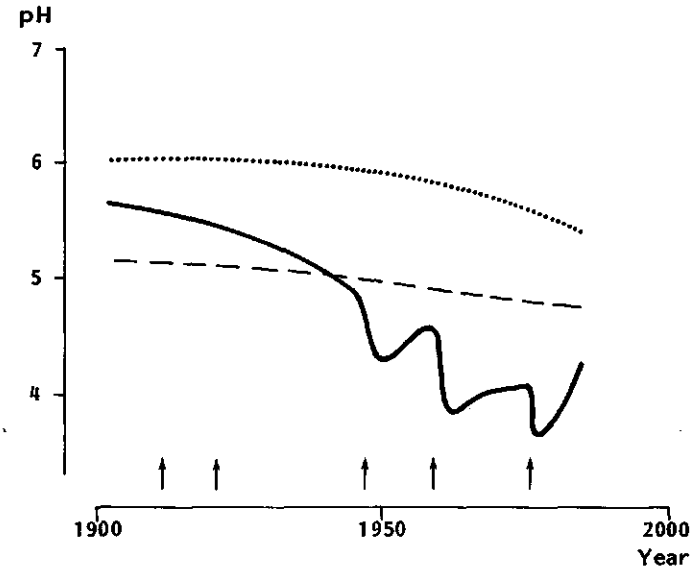

FIG. 8. Outline of long-term pH changes in moorland pools which dry up for a considerable part in extremely dry years (solid line), moorland pools which are permanently filled with water (broken line) and acidifying lakes in Europe and North America (dotted line). Arrows indicate extremely dry years.

will continue as long as (potential) acidifying substances (protons, ammonium) are added to the system in smaller proportions than sulphates and nitrates, which can act as potential alkalizing substances, provided that enough organic material for the reduction of sulphate and nitrate is present.

In those moorland pools where the bottom is permanently submerged, the rate of acidification is similar to that in the North-American and Scandinavian lakes.

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Een verkorte versie van dit artikel is aangeboden aan Freshwater Biology.

HOOFDSTUK 5

ACIDIFICATION OF A DUTCH MOORLAND POOL, A PALAEOLIMNOLOGICAL STUDY

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ABSTRACT

The Dutch moorland pool Achterste Goorven is undergoing rapid acidification. In the period 1925-1985 sediment core diatom inferred pH has fallen from 5.8 to 4.8. During the same period observed pH fell from 6 to 4.2 and plankton tow diatom inferred pH fell from 5.7 to 4.2. To date, this is one of the fastest documented rates of acidification of any pool or lake in temperate regions exposed to acid rain.

Our results indicate that useful stratigraphic information can be obtained from an analysis of the organic sediments of even a very shallow (mean depth 0.6 m) pool. Although there is evidence of downward displacement of sediments in such shallow water bodies, this process does not completely homogenize the sediment record. The accuracy of the reconstruction is substantially improved by a multidisciplinary approach.

INTRODUCTION

The present study constitutes an attempt to determine whether or not it is possible to reconstruct past events associated with moorland pool development during the last 150 years from an analysis of its submerged sediments. The purpose of the study was to test the application of palaeolimnological techniques in order to determine the rate of acidification in a shallow moorland pool from data assembled by a multidisciplinary team of scientists.

Moorland pools extend over much of western Europe from northwestern France to the Baltic and England (Moore & Bellamy 1973). The distribution of approximately 3500 moorland pools referred to as 'ven' (plural: 'vennen') in The Netherlands (not to be confused with fens which are more minerotrophic), is associated with the location of Pleistocene coversands. The moorland pools near Oisterwijk, where our study site is located, have been described by Heimans (1925), Coesel et al. (1978), Van Dam & Kooyman-van Blokland (1978) and Van Dam et al. (1981).

One of the first palaeoecologists to prove that useful stratigraphic information could be obtained from cores removed from shallow waters was Moss (1979, 1980). His study of the palaeoecology of a broad near Norfolk, England, established the validity of stratigraphic analyses for sediments of shallow water habitats.

The moorland pools of The Netherlands and the adjacent parts of Belgium and Germany present four major problems to the palaeoecologist:

1 They are very shallow, usually less than 2 m deep, with little topographic relief. As a result their entire sediment surface is frequently subjected to wind induced mixing. Wind also plays a major role in determining the morphometry of these pools and in controlling the distribution of their higher aquatic plants (Westhoff et al. 1973). In addition, high winds frequently deposit layers of fine sand at the mud water interface. This

sand acts to dilute the authigenic material deposited within the pool.

2 Bioturbation problems are augmented in moorland pools because in addition to the burrowing activities of numerous invertebrates typical of shallow tarns, bioturbation from vertebrate sources must also be considered. During droughts, shorelines encroach toward the center of the pool. As a result trampling by animals (e.g. roe, boar) and tourists often distorts the sediment stratigraphy of the exposed muds.

3 During periods of drought (e.g. 1921, 1959 and 1976, Buishand 1981) moorland pools in northern Belgium and The Netherlands lost a considerable part or even 100% of their volume due to evaporative losses and lowering of the groundwater table (Sykora 1979, Vangenechten et al. 1981). The exposed shoreline sediments of these pools were subject to desiccation and oxidation. Such conditions result in poor preservation of microfossils (Iversen 1969).

4 Sediment coring is often impeded by a dense aquatic vegetation cover, growing on top of the mud (e.g. mosses). If the vegetation cover is not removed before coring, the uppermost organic layers of sediment will be hopelessly distorted by the action of the core cylinder which forces the vegetation cover down into the flocculant organic material at the mud-water interface. In addition, the dense layers of plant fibres, needles, moss and higher aquatic plant rhizomes in the sediment may impede both coring and sectioning.

We have attempted to determine whether or not downcore changes in the abundances of diatoms could be correlated with known events which occurred in the surroundings of the moorland pool, Achterste Goorven, over the last 150 years. To this end we compared our sediment samples with an extensive series of plankton samples which were collected from this pool by the late Professor Dr. J. Heimans (University of Amsterdam) over the period 1925-1953. After 1975, the second author collected plankton samples from the very same sites visited by Prof. Heimans.

Pollen, fruits and seeds, algae and chironomid head capsules were analysed in order to provide some information about the origin and historical development of the pool. Old topographic maps of the study area were available to provide information about the land use in the surroundings of the pool over the last 150 years.

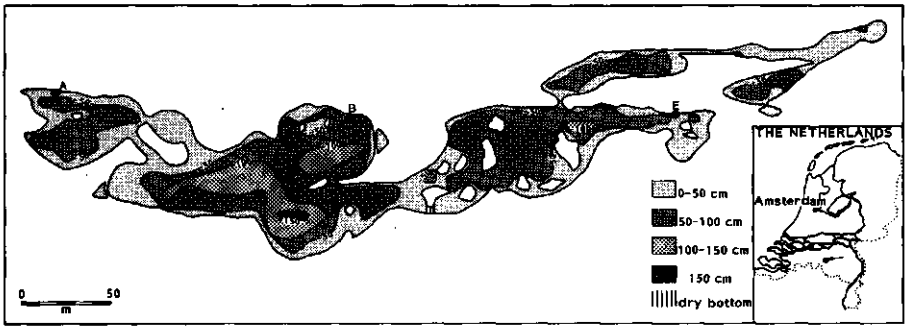

Figure 1. Bathymetric map of Achterste Goorven (11-13 September 1984) with its location in The Netherlands in the inset. Plankton tow and chemical sampling stations indicated with letters, coring stations with numbers.

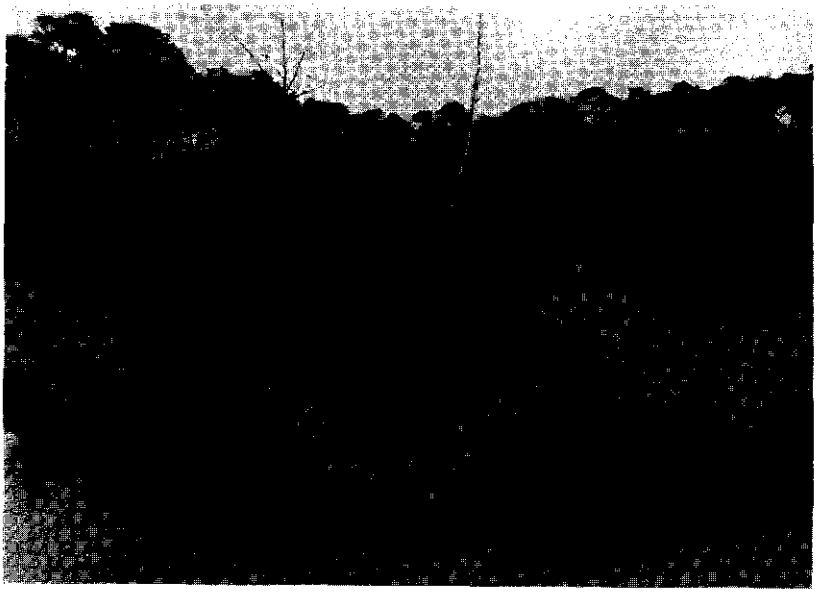

Figure 2. Looking east across the width of Achterste Goorven near station 7 where the ice was 10 cm thick (30 January 1985). The small island in the foreground has been colonized by Myrica gale, Molinia caerulea and Betula pubescens. Pinus sylvestris is the dominant species on a sand ridge at the background.

SITE DESCRIPTION

Achterste Goorven, located near Oisterwijk in the southeastern portion of The Netherlands, is a shallow moorland pool with low relief, a surface area of approximately 2.3 ha, and a mean depth of 0.6 m (Fig. 1). The pH of its surface waters ranges from 3.4 to 5.5 (median = 3.9), its sulfate content ranges between 12 and 68 mg l^{-1} (mean = 35 mg l^{-1}) and its calcium content between 1 and 11 mg l^{-1} with a mean of 4 mg l^{-1} over the period 1979-1984.

The dominant vegetation surrounding Achterste Goorven consists of Pinus sylvestris (the dominant arboreal pollen producer), Quercus robur, Q. rubra and Betula pubescens. The dominant grasses, Molinia caerulea and Deschampsia flexuosa, grow in close association with Calluna vulgaris, Erica tetralix and Vaccinium myrtillus. The pool itself is surrounded by a fringe of Myrica gale (Fig. 2). Mosses (e.g. Drepanocladus and Sphagnum species) play only a minor role in the cover of the shoreline vegetation around the pool. In the open water Nymphaea alba is the most conspicuous macrophyte but its floating leaves actually cover less than 1% of the total surface area of the pool. Patches of Juncus bulbosus are common along the shore.

METHODS

Sediment coring

Replicate cores were taken from Achterste Goorven at stations 4 and 7 (Fig. 1) during a period of ice cover on 30 January 1985. Both cores were taken with an Ali corer (Ali 1984). The acrylic coring tube's internal diameter was increased from 3.5 to 7 cm to permit removal of a larger quantity of sediment per core. The 24 cm long core removed from station 4 was extruded and sectioned at 1-cm intervals at the site while the 38 cm long core from station 7 was taken to the laboratory where it was frozen, extruded from its plastic liner and sectioned (also at 1-cm intervals) while frozen. The external stratigraphy of each core was described before sectioning.

Each of the 1-cm thick sections contained 38 ml of sediment. Half of this was used for Pb-210 analysis (A. van der Wijk). The remainder was split between B. van Geel (2 ml for pollen analysis), M. Dickman (2 ml for diatom analysis) and A. Klink (ca. 15 ml for macroinvertebrate analysis and selection of fruits, seeds and other macrofossils).

The percentage of inorganic material in the core was determined by loss of weight following its oxidation with concentrated HNO_3 and H_2O_2. Microscopic analysis of the inorganic material indicated that it was composed primarily of fine sand along with some diatom frustules and siliceous chrysophyte and poriferan spines.

The replicate cores, AG 4 and AG 7, from Achterste Goorven were analysed at a variety of depths to determine their downcore stratigraphy. However, for the sake of brevity, only those depths that all four researchers analysed together are emphasized in this paper. When not stated otherwise all of the results in this paper refer to core AG 7.

Pb-210 analysis

Pb-210 was measured through its alpha emitting granddaughter Po-210 using the isotope dilution technique (Flynn 1968, El-Daoushy 1981).

Ten ml of wet sediment was weighed and subsequently dried at 40°C for about 12 hours. Weight loss was determined and the ratio between wet weight and dry weight volume was established. Approximately 1 g of dry sediment was transferred to a 250-ml Kjehldahl flask. On occasion smaller samples were necessitated for lack of sediment. The material was gently boiled with concentrated HNO_3 to which 30% by volume H_2O_2 was added dropwise until brown fumes no longer emanated from the boiling liquid. The oxidized sediment was separated from the overlying liquid by centrifugation at 3000 rpm for 5 minutes. The residue was repeatedly washed with distilled water until no more color appeared. These washings were retained by transferring them to the beaker containing the original supernatant. The washed residue was then discarded.

After the addition of 100 microlitres of a Po-208 spike solution (activity 1 Bq ml^{-1}) the solution was evaporated to dryness in a 50-ml Teflon beaker. The remaining salts were chlorinated by dissolving them three times in concentrated HCl and evaporating the reactant until dry. The chlorinated salts were then redissolved in 20 ml of 0.5 N HCl to which 1 mg of ascorbic acid was added. After half an hour the solution was transferred to a Teflon plating cell (Van der Wijk & Mook, in press.) and Po was electroplated onto a silver disk by self-deposition at 85°C for 2 hours. The thinly plated samples were then measured in an alpha spectrometer for Po-208 and Pb-210 activities. Chemical yields from this procedure varied between 85 and 100%.

Diatoms

The term 'plankton tow diatoms' has a special meaning in this paper. It refers to diatoms collected with a standard plankton net. It does not refer to euplanktonic diatoms as these were never found in Achterste Goorven.

Initially (1925-1953) the plankton tow samples were taken with a 60 µm mesh net (15 cm diameter) by Prof. Heimans (A. van der Werff, pers. comm.). As the plankton net was towed through the water it collected considerable amounts of surficial bottom sediments as well as periphyton which was attached to the aquatic macrophytes which came in contact with the net. These samples were stored in the Hugo de Vries-Laboratory at the University of Amsterdam. After 1975 plankton samples were collected with a 40-µm mesh net of 20 cm diameter.

Both plankton tow and sediment diatoms were cleaned by boiling the raw material for 30 minutes in 30% by volume H_2O_2. To the sediment samples a known amount of polystyrene latex microspheres (mean diameter 8.7 µm, Coulter Counter Electronics Ltd.) was added for calculation of the concentration of each diatom (number per gram sand-free dry weight of sediment) according to the methods of Maher (1981). Plankton diatom counts are expressed only in terms of relative abundance. Slides were prepared by embedding the cleaned diatom valves in either Clearax or Hyrax mounting medium.

Slides were examined under oil immersion using a Zeiss Standard RA microscope equipped with phase contrast optics (N.A. = 1.30). All diatoms and microspheres within the field of view were counted according to the methods described by Berglund (1979) and Denys & Lodewijckx (1984). Random fields were counted on the slide until a total of 400 diatom valves had been recorded. The keys listed by Van Dam (1984) were used for identification.

The proportion that each diatom taxon comprises in the total assemblage was calculated as a percentage of the total and these results were used to estimate diatom inferred pH (Renberg & Hellberg 1982). The assignment of each diatom to a pH class was described in previous publications (Hustedt 1939, 1957, Renberg 1976, Van Dam et al. 1981, Dickman et al. 1984).

Chironomidae, seeds and fruits

Chironomid head capsules, fruits and seeds were analysed at 5 cm intervals down the length of the core. Using standard wire mesh sieves, each sediment sample was split into two size fractions: (1) > 500 µm and (2) 150-500 µm.

Macro-invertebrates and seeds were sorted using a standard dissecting microscope (x 80 magnification). Subsamples were taken from fraction 2 until a total of 300 chironomid head capsules had been removed. Half head capsules were included as halves in the tabulation of the data. The total chironomid densities were expressed per mg dry weight of organic matter.

Taxonomic keys for the identification of the chironomid head capsules were similar to those used by Moller Pillot (1984a, b) and Wiederholm (1983).

Pollen

In order to calculate pollen concentrations, Lycopodium tablets were added to the samples (Stockmarr 1971). The samples were treated with KOH and subsequently acetolysed (Faegri & Iversen 1975). Clay and sand were removed using a bromoform-alcohol mixture (specific gravity = 2.0). The organic material was embedded in glycerine jelly and sealed with paraffin wax. The

samples were searched for pollen, algal remains, Fungi, invertebrates, etc. (cf. Van Geel 1978; Van Geel et al. 1981, 1983). The occurrence (relative abundance) of all palynomorphs is expressed as a percentage of the total tree, shrub and upland herb pollen counts (Pollen). In most samples this total was more than 300 grains. Once this was accomplished, the remaining area of the slide was perused to glean more information about taxa represented in such low numbers that they had not previously been noted. Such taxa are identified by a '+' mark in all pollen diagrams.

RESULTS

Sediment core description

In both replicate cores (AG 4 and AG 7) the surface sediments (0-5 cm) were composed of a flocculant algal gyttja which was intermixed with very fine aeolian sands and coarse plant fibres, leaves, needles and even small twigs. From a depth of 5 to 10 cm the water content of these sediments decreased from 94% to 89% and finally to 20% near the base of the cores. For the sake of brevity, only the data from the AG 7 core are presented here (Table 1).

The percent inorganic content near the base of each core reached 79% by weight (Table 1). Below a depth of 15 cm the sand became coarser (mean grain diameter was 111 μm, n = 50). This coarser sand was yellow-brown in color and contained only a negligible number of diatom frustules. This is in sharp contrast to the very fine sands (mean grain diameter of 42 μm, n = 50) which were observed in the uppermost portions of the core where diatom frustules were relatively abundant.

Pb-210 analysis

Spectra obtained from Po-sources (Table 1) showed alpha resolution of 25 to 30 KeV. As a result, no corrections for peak overlap were required. Activities were determined in spike equivalents cm^{-2} to prevent the additions of extra inaccuracies resulting from our uncertainty concerning the absolute activity of the spike solution. Po-210 was assumed to be in

Table 1. The inorganic and organic composition of the 1 cm thick sediment samples. The Pb-210 estimated date of each of the sediment sections which were analysed is represented in the far right hand column. The volume/weight ratio is the volume (ml) in which 1 g of dry (organic and inorganic) material was distributed.

Depth (cm)	Water content (%)	Organic matter (%)	Inorganic matter (%)	Volume/Weight (ml g^{-1} dry material)	Pb-210 (spike eq cm^{-2})	Year AD
0-1	95.4	3.5	1.1	28.1		
1-2					3.66±0.08	1979-1983
3-4	93.7	4.5	1.8	18.4	7.20±0.70	1973-1978
4-5	94.3			20.2		
6-7	93.5	4.4	2.1	18.1	2.34±0.06	1951-1955
9-10	89.1	7.9	3.0	10.1	1.58±0.06	1929-1940
11-12	86.3	5.5	8.2	8.0	0.99±0.04	1914-1925
14-15	81.4	7.4	11.2	6.1	0.66±0.06	1884-1900
16-17	48.8	5.1	46.1	1.7	0.38±0.08	1855-1877
19-20	23.1	2.3	74.6	0.78	0.16±0.13	1836
20-21	35.5	1.4	63.1	0.92		
22-23					0.06±0.06	1816
23-24	20.0	1.5	78.5	0.86		

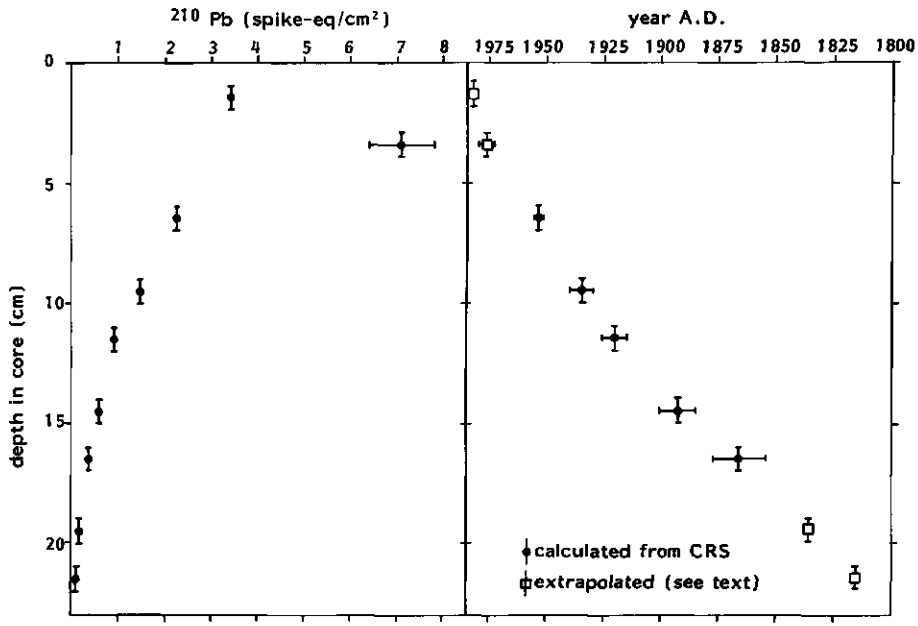

Figure 3. Pb-210 activity and age-depth downcore profile. Pb-210 activities expressed as spike-equivalents cm^{-2} (see text).

secular equilibrium with Pb-210.

Downcore sediment profile age determinations (Fig. 3) were determined using the constant rate of supply (CRS) model (Goldberg 1963, Oldfield et al. 1978). A problem to this was the apparent low Pb-210 activity at 1-2 cm depth, most probably caused by infiltration of freshwater, in which Po-210 and Pb-210 are not yet in radioactive equilibrium, into the interstitial waters of the surface sediments. This 'mixing layer' may extend to ca 4 cm depth as is indicated by the data obtained from our replicate core AG 4 (Van der Wijk & Mook, unpublished data).

Because of lack of reliable data in the 0-3 cm layer it was assumed that the average rate of deposition of organic matter in the 6-15 cm layer could be extrapolated to this layer (open squares, Fig. 3). Then these extrapolated ages were used as a reference for further age determination using the CRS model. Integration of the downcore Pb-210 activity profile was achieved by interpolation and numerical integration. Open squares (Fig. 3) were also used to denote downcore sediment age extrapolations below 17 cm because below this depth the Pb-210 integrated activity approached the total integrated activity which resulted in a large amount of uncertainty in the age determinations.

The average atmospheric Pb-210 fall out was estimated from the total integrated Pb-210 activity. The obtained value (0.029 pCi cm^{-2} yr^{-1}) was considerably lower than the average for the northern hemisphere (0.21 pCi cm^{-2} yr^{-1}, Crozaz et al. 1964). It was also lower than the atmospheric Pb-210 fallout estimated from the Pb-210 activity profiles of other nearby moorland pools (0.17 pCi cm^{-2} yr^{-1}, Van der Wijk & Mook, unpublished data).

Table 2. Relative abundance of the most common diatoms in plankton tow and sediment samples. For the plankton tow samples from station B the mean relative abundance of a number of samples is represented. The estimates of diatom inferred pH, diatom valve densities, dominance percentage and the average number of taxa observed during a count of 400 diatom valves are given at the bottom of the table.

	SEDIMENTS										PLANKTON TOWS		
core	AG7	AG4	AG7	AG4	AG7	AG7	AG7	AG7	AG7	AG7			
nr. of samples											4	3	5
depth (cm)	0-1	1-2	4-5	4-5	6-7	9-10	11-12	14-15	19-20	23-24			
period											1983-'84	1930-'53	1925-'29
Acidobiontic taxa													
Brachysira serians	0.75	5.0	1.0	-	0.75	-	-	-	-	-	-	-	-
Eunotia exigua	36.0	21.0	9.0	10.25	3.0	1.75	1.0	5.25	16.0	-	80.44	0.75	-
Frustulia rhomboides var. saxonica	8.75	7.75	10.25	6.75	9.0	8.0	4.0	9.0	10.5	100.0	2.0	13.67	9.45
Navicula 'hoefleri'*	2.5	1.0	0.5	0.5	0.5	0.25	0.5	-	-	-	0.13	-	-
Tabellaria quadriseptata	6.25	8.0	3.5	6.5	5.0	6.25	1.75	1.0	6.0	-	1.5	8.75	0.2
others	-	-	-	-	0.75	-	1.25	-	-	-	0.19	0.20	0.04
Subtotals	54.25	42.75	24.25	24.0	19.0	16.25	8.5	15.25	32.5	100.0	84.26	23.37	9.69
Acidophilic taxa													
Brachysira brebissonii	0.25	1.5	1.75	0.25	2.75	-	0.75	1.0	0.25	-	0.06	5.0	1.4
Cymbella gracilis	0.25	1.25	3.75	3.75	2.25	2.25	2.0	2.75	0.5	-	-	0.83	2.2
Eunotia elegans	3.5	7.75	6.0	6.75	4.25	2.5	1.5	3.25	4.5	-	0.13	0.92	2.25
Eunotia flexuosa	2.0	1.25	1.5	1.75	-	1.5	0.25	0.75	1.25	-	-	-	0.05
Eunotia incisa	7.0	7.75	8.5	6.75	7.0	6.25	2.25	5.5	1.25	-	1.06	26.75	1.4
Eunotia naegelii	1.25	1.0	2.25	2.25	0.5	2.0	0.75	1.5	1.0	-	-	0.25	0.1
Eunotia pectinalis varieties	1.25	4.0	1.75	1.25	2.0	3.25	3.5	2.5	0.25	-	-	-	1.15
Eunotia rhomboidea (symm. and asymm. forms)	6.0	3.25	1.0	6.75	1.75	3.75	2.75	3.75	3.5	-	1.06	4.17	0.5
Navicula leptostriata (=N. heimansii)	2.0	3.0	5.25	3.75	5.75	2.25	1.75	1.25	6.0	-	0.31	2.0	20.85
Navicula mediocris	2.5	1.75	0.75	0.75	1.75	0.75	1.5	1.0	1.75	-	0.31	1.25	1.65
Peronia fibula	0.75	-	2.0	0.75	2.25	-	0.25	2.25	8.5	-	-	0.83	1.25
Stauroneis anceps f. gracilis	0.75	0.5	0.5	0.75	-	0.75	0.25	2.0	1.75	-	-	-	0.05
Tabellaria flocculosa	0.75	2.25	1.75	1.25	0.5	0.75	1.0	1.5	4.25	-	-	0.58	1.65
others	-	-	-	-	2.75	0.5	0.5	0.5	0.25	-	0.06	1.67	0.40
Subtotals	28.25	35.25	28.25	36.75	33.5	26.5	19.0	29.5	35.0	-	3.0	44.25	34.9
Circumneutral taxa													
Achnanthes minutissima	0.5	1.5	3.5	7.0	5.0	8.5	19.0	9.0	4.5	-	0.13	0.67	0.9
Brachysira vitrea f. lanceolata	4.25	6.25	8.0	9.0	10.0	14.5	24.5	18.5	14.0	-	0.5	5.5	11.35
Eunotia bilunaris	3.5	1.5	4.5	0.5	2.75	5.0	2.5	3.5	0.75	-	8.6	8.08	2.95
Fragilaria virescens	0.75	7.0	14.0	12.75	15.25	14.25	5.75	9.25	2.75	-	2.8	12.5	21.3
Navicula pupula	-	-	-	-	-	-	1.25	-	-	-	-	-	-
Navicula radiosa	-	-	-	-	-	-	1.25	-	-	-	-	-	-
Nitzschia kamptschiana	0.75	0.75	1.0	0.25	-	2.25	-	-	0.25	-	-	0.33	-
Pinnularia abaujensis	0.75	0.5	0.5	2.25	0.75	1.75	0.25	3.5	0.5	-	-	0.17	-
Pinnularia biceps	1.75	0.5	2.75	3.0	2.5	5.50	1.0	5.0	4.75	-	0.13	0.17	0.1
Pinnularia microstauron formae	1.25	1.0	0.5	-	0.75	-	-	-	-	-	-	0.17	-
others	-	-	0.5	0.5	-	0.5	0.5	0.25	-	-	0.06	0.83	0.95
Subtotals	13.5	19.0	35.25	35.25	37.0	52.25	56.0	49.0	27.5	-	12.22	28.42	37.55
Alkaliphilous taxa													
Cymbella microcephala	1.0	0.5	0.75	0.75	2.75	0.25	9.5	2.0	2.0	-	0.13	0.5	1.1
Gomphonema angustatum	-	-	-	-	-	-	1.75	-	-	-	-	-	-
Nitzschia perminuta	3.0	2.75	3.0	3.25	7.75	4.75	3.0	4.25	2.75	-	0.13	1.08	14.55
others	-	-	-	-	-	-	0.5	-	-	-	-	0.92	1.35
Subtotals	4.0	3.25	3.75	4.0	10.5	5.0	14.75	6.25	4.75	-	0.25	2.5	17.0
Unclassified taxa	-	-	-	-	-	-	1.5	-	-	-	-	0.42	-
Diatom valve concentration (10^7/g dry wt)	3.7	4.9	4.4	0.61	-	5.1	-	0.79	0.43	0.0008	-	-	-
Total number of valves counted	400	400	400	400	400	400	400	400	400	1	1600	1200	2000
Number of taxa in count	30	29	31	29	26	28	37	28	28	1	13.15	24.7	23.0
Dominance percentage	36.0	21.0	14.0	12.75	15.25	14.5	24.5	18.5	14.0	100	80.4	28.0	27.9
Renberg inferred pH	4.8	4.9	5.2	5.2	5.5	5.5	5.8	5.5	5.1	-	4.2	5.1	5.7

*sensu Ross & Sims (1978)

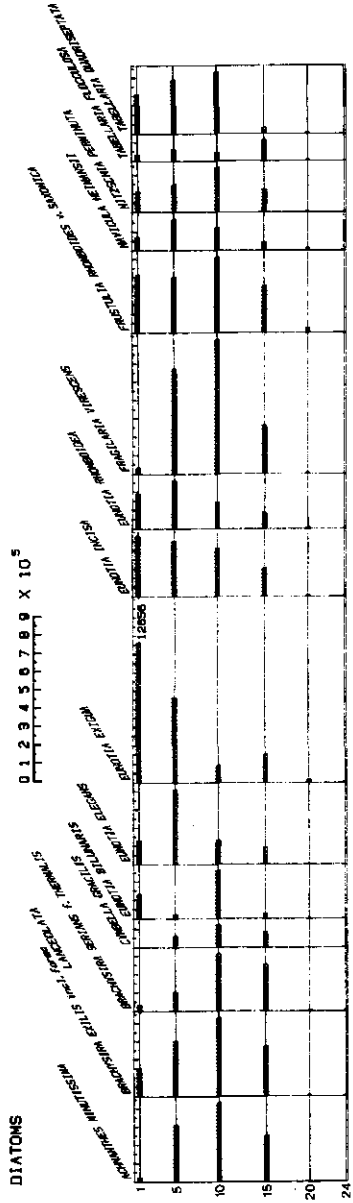

Figure 4. Downcore distribution of diatoms. Densities are expressed as the number of diatom valves per gram of sand-free dry weight (Brachysira exilis should be B. vitrea).

Diatoms

Diatom nomenclature is in a constant state of flux. Recently, for example, Round and Mann (1981) transferred the small Anomoeoneis spp. to the genus Brachysira. Ross (in Hartley 1986) renamed and changed the taxonomic ranks of a few of the infraspecific taxa, with exception of A. exilis forma lanceolata Mayer. As we frequently found it in our samples, we were obliged to rename it as B. vitrea forma lanceolata Van Dam. In this paper, Eunotia rhomboidea Hustedt refers to both Eunotia rhomboidea and E. tenella as interpreted by Van Dam et al. (1981). Eunotia bilunaris (Ehrenberg) Nörpel is the correct name for E. lunaris (Ehrenberg) Grunow (M. Nörpel pers. comm.).

It was impossible to separate the species Navicula subtilissima Cleve and N. pseudosubtilissima Manguin using the light microscope. They are combined in this study as Navicula subtilissima. Fortunately their ecology is very similar (Germain 1982).

The mean relative abundance of plankton tow diatoms from station B calculated for the periods 1925-1929, 1950-1953 and 1984-1985 was based on 5, 3 and 4 samples respectively (Table 2). The data have been organized into pH categories (Hustedt 1939) and the dominant diatoms are given for each of these categories (Table 2). Alkalibiontic taxa were absent from all of our Achterste Goorven sediment samples. Diatom inferred pH based on the formula of Renberg and Hellberg (1982) was also calculated and placed in the table as were species richness and dominance. The latter were used as indicators of biotic diversity, as discussed by Van Dam (1982).

The relative abundance of the acidobiontic species increased from the earliest plankton tow sampling dates (1925-1929) until the present when over 80% of the diatoms in the sample were acidobiontic taxa (Table 2). Initially Frustulia rhomboides var. saxonica and Tabellaria quadriseptata accounted for most of the aci-

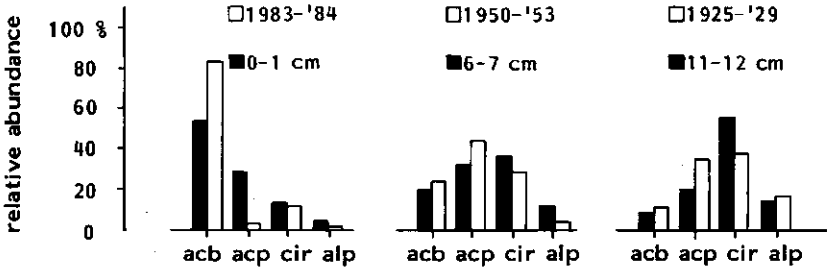

Figure 5. Histograms of the relative abundance of acidobiontic, acidophilic, circumneutral and alkaliphilous diatoms at 0-1 cm (1983-1984), 6-7 cm (1953-1955) and 11-12 cm (1925-1929).

dobiontic taxa. After 1955, however, Eunotia exigua, which was the most sulfate and acid tolerant species (Van Dam et al. 1981, Descy 1984), completely dominated the plankton tow diatom samples. Acidophilous taxa increased from the 1920s (35%) to the 1950s (44%). During the 1950s Eunotia incisa was the dominant diatom.

The concentration of diatoms per g sand-free dry weight increased downcore in the top 10 cm of the core and then decreased as the sand content of the sediments reached 95%. Diatom densities in the top 20 cm of sediments ranged between 0.43 and 5.1 x 10^7 diatom valves per g sand-free dry weight (Table 2). Below 20 cm the diatom density suddenly decreased to 7600 valves per gram sand-free dry weight.

The alkaliphilous diatom Nitzschia perminuta declined in absolute as well as relative abundance above a sediment depth of 9 cm (Fig. 4 and Table 2). This was also true for the circumneutral diatoms (e.g. Fragilaria virescens and Brachysira vitrea forma lanceolata) which declined upcore as diatom inferred pH fell from 5.5 to 4.8. The absolute abundance of a number of the acidophilous and acidobiontic taxa, on the other hand, increased upcore (Fig. 4 and Table 2).

The rate of lake acidification was inferred from the shift in downcore diatom species composition and from the inferred pH of the plankton tow diatoms recovered from Achterste Goorven in the 1920s, 1950s and 1970s. The relative abundance of acidobiontic taxa (acidophilic and circumneutral taxa) and alkaliphilic taxa as well as those for which no pH category could be assigned was calculated for both the plankton tow diatoms (open bars) and sediment core diatoms (solid bars). Three time periods are displayed for both the plankton tow and the sediment core diatoms (Fig. 5).

The plankton tow and sediment core diatom inferred pH estimates can be compared with the actual measures of pH for Achterste Goorven (Fig. 6). The downward displacement of Eunotia exigua as illustrated in Fig. 7 is discussed in a later section.

During the period 1952 to 1984 the observed pH at station A (Fig. 1) fell from 5.2 (P. van Oije, unpublished data) to 4.0 (Fig. 6). The plankton tow diatom inferred pH calculated from the B Index (Renberg & Hellberg 1976) for the same station (A) fell 1.2 of a pH unit from 1925 to 1955 and 0.8 of a pH unit during the period 1955 to 1984. At station B, which was located near station 4, the pH as measured with colorimetric techniques by J. Heimans (unpublished data) fell from 6.0 (mean of 3 measurements during the period 1919-1926) to 4.2 (mean of 4 potentiometric pH measurements during the period 1983-1984). The plankton tow diatom inferred pH at this site fell

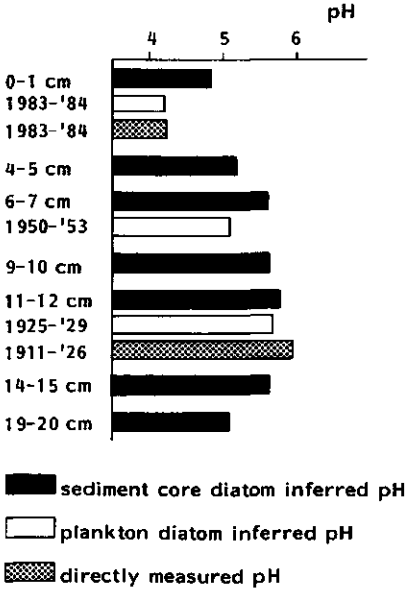

Figure 6 (left). Comparison of diatom-inferred pH and observed pH.

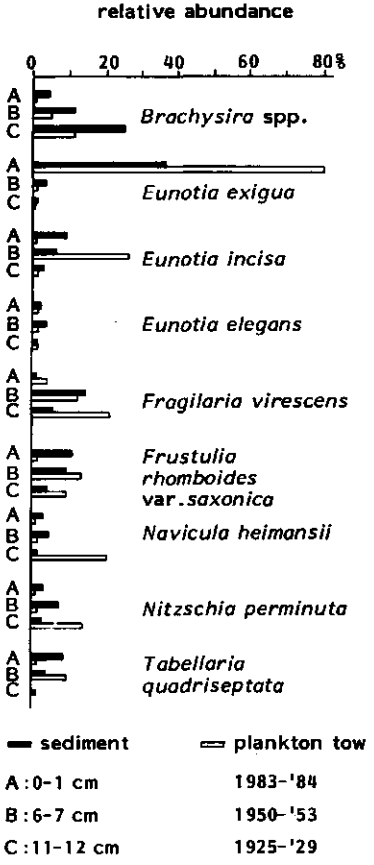

Figure 7 (right). The relative abundance of the 9 most abundant diatom taxa in the plankton (open bars) and sediments (solid bars) during the period 1925-1985. The relative abundances of diatom taxa at different sediment depths are plotted against the means for the plankton diatoms collected in corresponding periods. Correspondances are based on Pb-210 analyses (Fig. 3).

from 5.8 to 4.2 over the last 60 years. There is excellent agreement between the plankton tow diatom inferred pH data set and the observed changes in pH in Achterste Goorven over the period 1925 to 1984.

Chironomids

Chironomid head capsules were examined at four depths: 15-14 cm, 10-9 cm, 5-4 cm and 1-2 cm. Below 15 cm only negligible quantities of chironomids were found. A survey of all encountered taxa, organized by subfamily, is given in Fig. 8a.

In Figure 8b the most common taxa are organized in three groups: the Psectrocladius psilopterus assemblage, the Cladopelma assemblage and the Chironomus assemblage. These assemblages are named after their most abundant

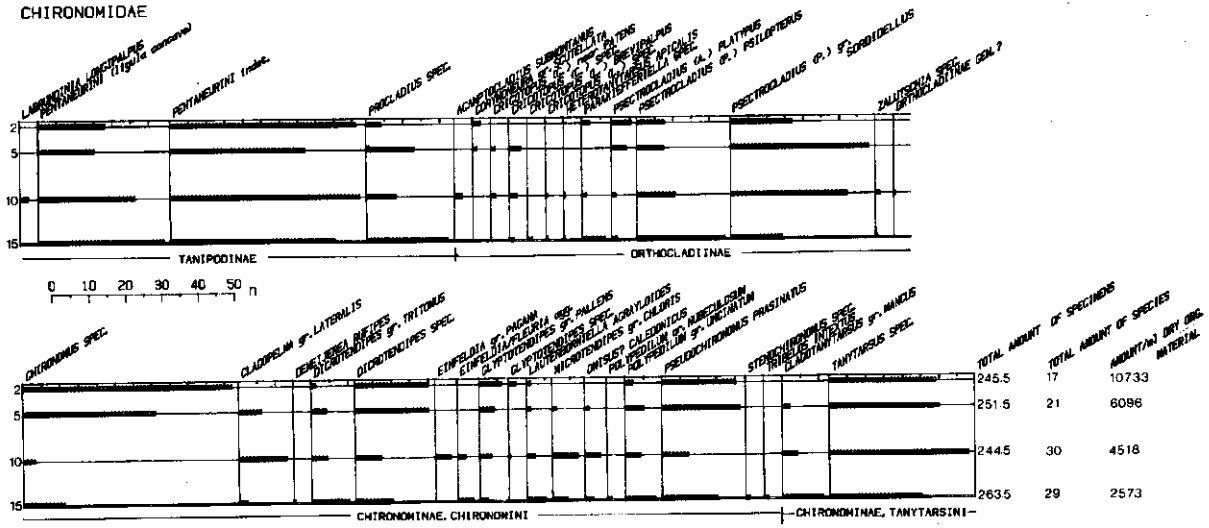

Figure 8a. Numbers of chironomid head capsules counted at four depths and total amount of species.

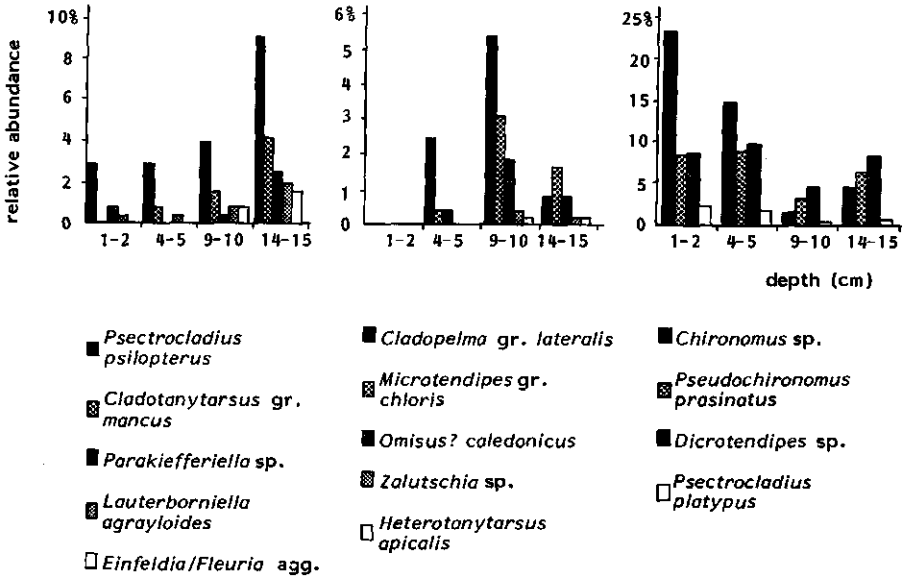

Figure 8b. Relative abundances of the most prominent chironomid taxa, organized into three assemblages.

representatives.

The Psectrocladius assemblage, which has its optimum in the 14-15-cm layer, is typically found in oligohumic, mesotrophic lakes (Brundin 1949, Saether 1975). The Cladopelma assemblage, which was most abundant in the 9-10-cm layer, has never been reported alive from The Netherlands. Brundin (1949) observed this assemblage in three oligotrophic lakes with various concentrations of humic acid. The Chironomus assemblage has its optimum in the topmost layer of sediment. Chironomus may be dominant in very diverse habitats: extremely eutrophic lakes and dystrophic pools (Saether 1975, Wiederholm 1983). Psectrocladius platypus is a definitely acidobiontic species (Moller Pillot 1984b), while Pseudochironomus and Dicrotendipes can tolerate pH-values as low as 3.4 (Leuven et al. in press).

An upcore shift is recorded from a meso- to an oligotrophic environment. Above 5 cm depth acidification is apparent.

Pollen and plant macrofossils

Major changes in the vegetation around Achterste Goorven over the last 150 years are evident from the pollen stratigraphy of its sediment core. Separate pollen profiles for all recorded taxa are provided (Fig. 9) to permit the recognition of downcore pollen patterns. The main trends in the relative abundance (percentage composition) of pollen of upland herbs, cultivated plants and arboreal taxa have been illustrated in an Iversen styled summary diagram (Fig. 10).

Although pollen percentages cannot be directly interpreted in terms of percentage cover, downcore changes in percentage composition can be used to indicate major temporal trends in vegetation types over the last 150 years in this region (e.g. changes in the intensity of land use for agriculture).

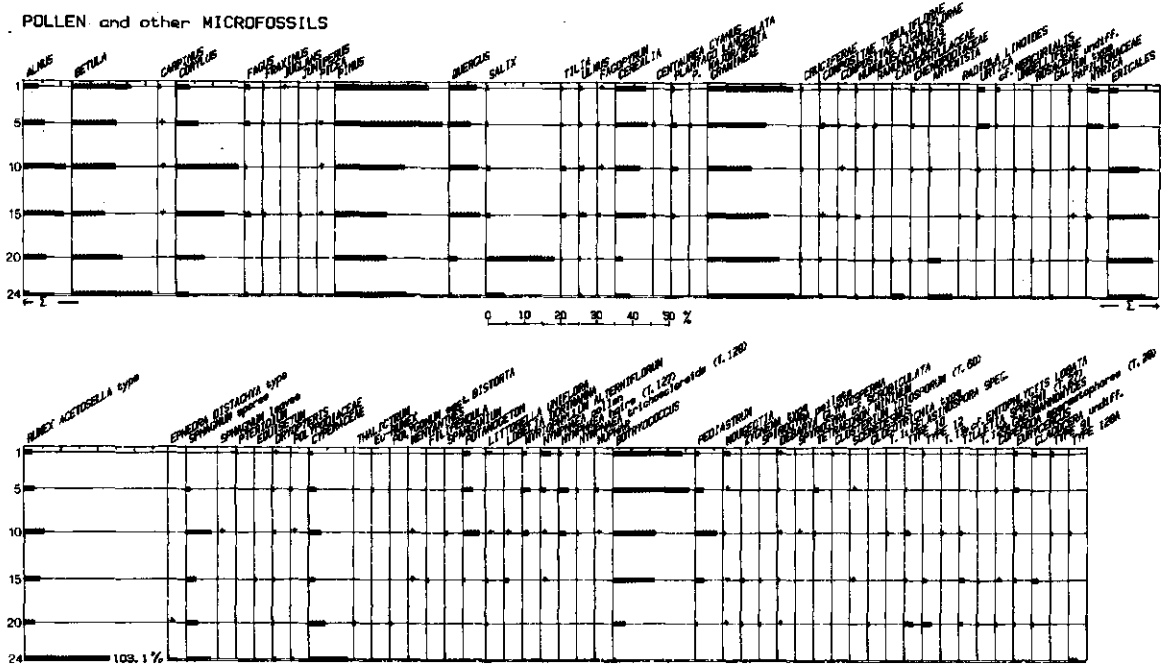

Figure 9. Downcore percentage pollen and microfossil distributions. For each pollen type the relative abundance is plotted.

Specific details of the downcore changes in relative abundance are noted in the discussion section.

In addition to the relative abundance of pollen its downcore concentration (Fig. 11) was calculated to permit us to gain a general impression of pollen and sediment influx.

The seeds, fruits and other botanical macrofossils (Fig. 12) were recorded in order to gain additional information about local changes in species composition in, and near Achterste Goorven.

DISCUSSION

Recent acidification

Belgium and The Netherlands are located in the very centre of the European

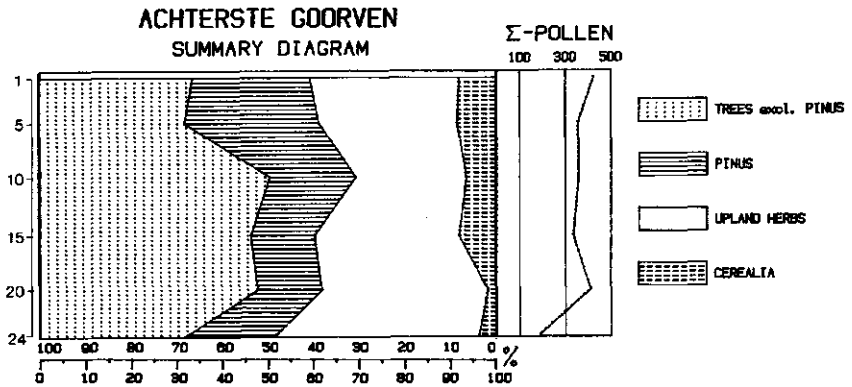

Figure 10. Iversen styled diagram for pollen of trees, upland herbs and Cerealia.

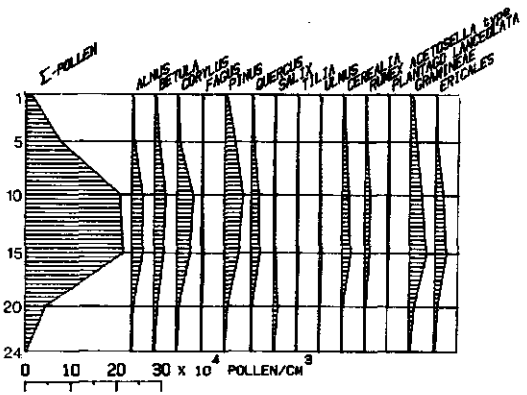

Figure 11. Pollen concentration diagram (no. of pollen grains per ml) for 14 taxa.

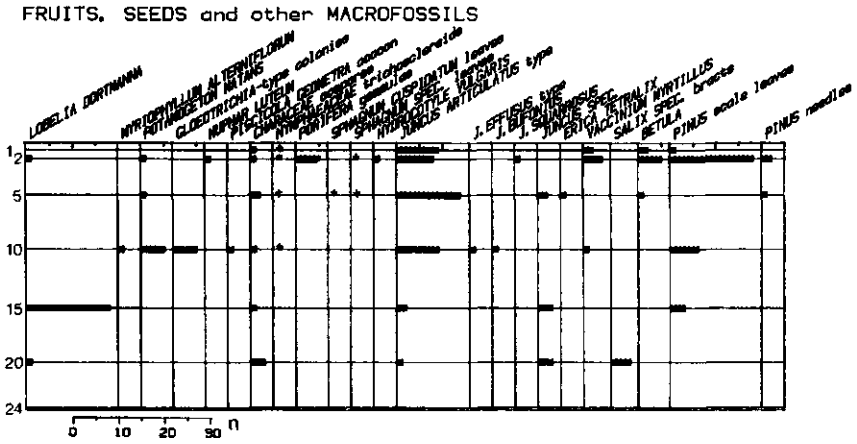

Figure 12. Diagram of fruits and seeds and other macrofossils from Achterste Goorven.

acid rain region (EMEP/CCC report 1984). Measurements of the pH in the rainwater at the nearest precipitation monitoring stations, located approximately 20 km from our study area, gave a mean pH for the period 1978-1982 of 4.4 (KNMI-RIV 1983). The mean sulfate sulfur concentration for the same period was 7.1 mg l^{-1} and the mean ammonium nitrogen concentration was 1.7 mg l^{-1} (ibid.). Most of the nitrogen is in the form of ammonium. The mean sulfur dioxide sulfur concentration in the air near Achterste Goorven, according to the Netherlands National Air Pollution Network for the period 1978-1984 was 10.3 $\mu g\ m^{-3}$. This results in the very high deposition rate of about 160 kg S $ha^{-1}\ y^{-1}$. Accordingly the mean sulfate sulfur concentration in the pool during the period 1979-1984 was very high with 12 mg l^{-1} as an average of 23 measurements.

Battarbee (1984), reviewing the available studies on diatoms and lake acidification, concludes that the evidence generally indicates that lake acidification is due to an increase in the acidity of precipitation as a result of emissions from fossil fuel combustion. The average decline of the pH, as inferred from diatom data from 34 lakes in Scandinavia and North America was 0.6 units. The onset of acidification was generally between 1920 and 1950, but in one Norwegian lake the acidification already began in 1850.

Berge (1975, 1979), Renberg & Hellberg (1982), Tolonen & Jaakkola (1983), Davis et al. (1983), Flower & Battarbee (1983) and Battarbee et al. (1985) describe the changes in the species composition of diatom assemblages in cores of acidifying lakes in Scandinavia and Scotland. In all cases acidophilous and acidobiontic species are increasing from the bottom to the top of the sediments. Particularly in Scandinavia species like Brachysira serians, Eunotia bactriana, E. denticulata, Navicula subtilissima and Semiorbis hemicyclus are abundant or dominant in the surficial sediments of acidified lakes. Tabellaria binalis increases by acidification both in Scandinavia and Scotland, while T. quadriseptata, Navicula hoefleri and Eunotia incisa seem to be more dominant in the surficial sediments of the Scottish lochs. E. exigua generally is of minor importance in the discussed lakes. In contrast this species is the most dominant one in the surficial sediment of Achterste Goorven. The other abundant taxa in the 0-1-cm

sediment of Achterste Goorven are very similar to those in Scandinavia and Scotland (e.g. E. incisa, Tabellaria quadriseptata and Navicula hoefleri). The absence of Tabellaria binalis from Achterste Goorven was interpreted as indicative of a preference of T. binalis for sandy substrates. Species like Eunotia bactriana and Semiorbis hemicyclus have never been found in The Netherlands. The absence of the latter species may be associated with its preference for deeper waters, which are rare in The Netherlands. The dominance of Eunotia exigua, which is very resistant to acidification (Van Dam et al. 1981) is not matched by lakes in other parts of Europe.

Our data indicate that the rate of acidification is among the highest reported to date. Both plankton tow and sediment diatom inferred pH, as well as direct observations of pH (Fig. 6) demonstrate that the pH declined from about 5.8 to ca 4.2 over the last sixty years. Also the subfossil Chironomid assemblages indicate a recent decrease of pH in this shallow pool. Two major factors are responsible for this high rate of acidification. Firstly the small volume causes large parts of the bottom of the pool to dry up during periods of drought, resulting in oxidation of the reduced sulfur compounds in the sediment. Therefore, sulfate concentrations are high after refilling (Vangenechten et al. 1981). Secondly the atmospheric deposition of acidic substances is very high in this region.

During the early 1900s a large standing crop of macrophytes was present in the pool, as indicated by the seeds and fruits in the sediments and the early records of the pool's vegetation. The abundant vegetation was a good substratum for diatoms, which had a high density in this period (Fig. 4). Also the chironomids attained the maximum density during this period (Fig. 8a). As the pool acidified the macrophyte standing crop declined and with it the chironomid head capsule diversity and the diatom valve density and diversity.

The pH decline in Achterste Goorven is very similar to that in Härsvatten in southern Sweden (Renberg & Hellberg 1982). As far as we are aware only a number of small ($\bar{a}$ = 59 ha), but relatively deep ($\bar{z}$ = 10.3 m) lakes near Gothenburg is acidifying faster than Achterste Goorven and other moorland pools in The Netherlands. In these lakes pH declined from 6.6 in 1968 to 4.7 in 1979 (average of 18 lakes) and increased slightly afterwards (Morling 1981, 1984).

Before the period of falling pH in Achterste Goorven, the data indicate an increase of pH from the bottom of the core to a depth of ca 12 cm. This, and also the fact that only rather young sediments (age less than 200 years) were found can only be understood after reconstruction of the local history of the moorland pool which will be discussed in the next section.

Historical development

Below 20 cm

The pool Achterste Goorven probably originated during the Late Glacial period as a depression in the landscape and was filled up with peat deposits in the Postglacial (Geenen 1977). The peat was later excavated by man, for use as a fuel. The code for the village of Oisterwijk from the year 1509, which was published by Posthumus (1911) already contained regulations for the excavation of peat from the 'Goer', of which the Achterste Goorven is a part. Documents were found in the archive of the village of Oisterwijk and the National Archive in 's-Hertogenbosch dating from 1724, 1746 and 1823 in which farmers were allowed to excavate peat from the 'Goor'.

The Voorste Goorven (CP I in Fig. 1 of Van Dam & Kooyman-van Blokland

1978) was the other part of the ancient 'Goer', 'Goir' or 'Goor'. Nowadays it is separated from the Achterste Goorven (A I in the same figure) by a narrow dam with a culvert, which allows drainage of water during times of high water levels from the Achterste Goorven to the Voorste Goorven. Counting annual rings of the stubs of cut Scots pines on the dam indicated that this dam is at least hundred years old. According to the code of 1509 the peat-diggers were allowed to construct dams through the moorland pools in order to facilitate the transport of the peat, although it was usual to remove the dams after completion of the peat excavation.

The past connection of Achterste Goorven with Voorste Goorven was important for the determination of the composition of the water in Achterste Goorven. Originally the water of the pools in the very nutrient poor sands near Oisterwijk was oligotrophic and badly suited for any economic purpose, e.g. fish stocking. Therefore, the Voorste Goorven was fertilized with agricultural drainage water, which was supplied through ditches (see Fig. 1 in Van Dam & Kooyman-van Blokland 1978). As early as 1619 the Board of Oisterwijk allowed a citizen to prepare the Witven (CP II in the same figure), which receives the drainage water of Voorste Goorven, for stocking with carps, as appears from an old deed in the State Archive. One may suppose that the trophic state of the Voorste Goorven increased with time, with the intensification of agricultural practice. According to the assemblages of desmids and diatoms in the beginning of this century Voorste Goorven contained mesotrophic water (Heimans 1925, Coesel et al. 1978, Van Dam & Kooyman-van Blokland 1978).

Also important for the interpretation of the present core are the changes of the terrestrial vegetation in the surroundings of Achterste Goorven. The rotational burning of heather coupled with its overgrazing by sheep in the late Middle Ages, the burrowing of rabbits into the hillsides and the hagging of peat were all factors contributing to soil erosion following the felling of the trees in the province of Brabant. The sand so liberated was probably gathered into bare wandering dunes which moved in the direction of the prevailing winds whenever these exceeded a speed of 16 km h^{-1} (Burnett 1964).

The deepest sediments (24-34 cm) in the Achterste Goorven core contained representatives of non-aquatic species (Fig. 9). Terrestrial pollen at 24 cm was associated with large quantities of wind blown sand. All the evidence to date indicates that these sands were deposited over a relatively short period of time (i.e. less than 50 yrs) prior to dune stabilization in the Oisterwijk region. It is hypothesized that these sands partially filled up the peat excavated basin of Achterste Goorven in the early 1800s. The occurrence of a coarse sandy sediment below 20 cm (see sediment core description) reflects erosionary processes in the surroundings of the sample site. The relatively high pollen percentage of the dicot pioneers Rumex acetosella and Artemisia is typically associated with the regular occurrence of bare soils which are formed as a consequence of these erosionary processes. The very low representation of algae and other water plants in this layer indicates that the sediment and its microfossil contents represents a non-aquatic habitat. We have interpreted this as an indication that the sediments of Achterste Goorven below a depth of 20 cm probably represent a terrestrial or semiaquatic condition, at least at the sample site (station 7) located near the center (Fig. 1). Below a sediment depth of 20 cm diatom valve concentrations dropped three orders of magnitude (from $0.43\text{-}5.1 \times 10^{7}$ to 7.6×10^{4} valves per gram sand-free dry weight, Table 2). According to the Pb-210 data this sand layer was deposited ca 1810-1820, which is in agreement with the date of 1823 when the last document found in

which farmers were allowed to excavate peat was issued (see above).

Until the past century the Oisterwijk region was poor in forest, although small lots of forest with various tree species and especially Scots pines on the dryest spots have always been present. Stabilization by afforestation of the dunes and heathlands began in the late 1700s and culminated about a century later. In several sites in the sandy Flanders and the province of Brabant, Pinus was already planted at the end of the 17th century (Beyens 1984). The dunes on the shores of Achterste Goorven were afforested with pines between 1830 and 1840 (Van Hees & Van den Wijngaard 1976). As a result of the absence of Pinus (or at least its very infrequent occurrence) in The Netherlands during the late Holocene a sudden increase in pine pollen in recent sediment core pollen spectra can be used to indicate pine plantations (Janssen 1972). From the Pinus-pollen profile for Achterste Goorven (Fig. 10) it is evident that the aquatic sediments of this pools were deposited after the planting of Pinus sylvestris in the area. The Pb-210 date of ca 1816 at the bottom of the core in this context seems to be a little too old.

The percentage of herbaceous pollen, especially Ericaceae, grasses, cereals, buckwheat and weeds like Rumex acetosella and Plantago lanceolata indicate that the forested area near Achterste Goorven was primarily an open forest, i.e. patches of forest intermixed with heathlands and arable fields, which is in accordance with the pattern of land use that is registrated on the topographic maps of 1835 and 1840.

20-15-cm depth

The sample at 20 cm depth, dated with Pb-210 at ca 1830-1840 contains Salix pollen at its maximum densities in the core (Fig. 9). Also bracts of Salix were found, indicating that willows were temporarily present at or near the sample site. The aquatic plants represented at this depth (20-15 cm) were Lobelia dortmanna, Littorella uniflora, Characeae, Botryococcus, Pediastrum, and spores of Zygnemataceae (Debarya, Mougeotia, Spirogyra, and Zygnema, Fig. 12). The pH, inferred from the sediment core diatoms, rose in the period of deposition of the 20-15-cm depth layer from 5.1 to 5.5 (Fig. 6).

15-10-cm depth

Samples from 15 cm to the top of the deposit represent true pool depositions. Some macrofossils from vegetation around the pool were also embedded in the sediments (e.g. Vaccinium myrtillus, Pinus and Juncus spp.). The seeds of the Juncus articulatus type (Körber-Grohne 1964) were probably produced by J. bulbosus, which is presently common nearshore. Myrica gale and J. bulbosus are both examples of plants which were probably common inhabitants along the fringe of the pool in former times, as they are still now.

The presence of the seeds of Lobelia dortmanna at 15-cm depth (circa 1890) in Achterste Goorven sediments (Fig. 12) was significant. The habitat of this taxon is characterized by sandy soils, oligotrophic water and fluctuating water levels (Schoof-van Pelt 1973). These are precisely the conditions which are associated with a number of taxa from the Psectrocladius psilopterus chironomid assemblage which reach peak abundance at 14-15 cm (Fig. 8b). Lobelia dortmanna was not found above 15 cm with the exception of a single seed recorded at 2 cm. Characeae oospores were frequently associated with Lobelia dortmanna but the Characean species were found at all depths that we examined (Fig. 12). The upcore disappearance of Lobelia may be related to the development of an organic mud layer which is

inimical to the growth of this species (Westhoff et al. 1973).

The samples from above the 15-cm level display relatively high pollen percentages of Potamogeton (seeds of P. natans). Nymphaea, Nuphar luteum and Myriophyllum alterniflorum were also found (Fig. 13). The species that were recorded from these levels were also recorded by naturalists, who visited Achterste Goorven during the first decennia of this century (e.g. Thijsse 1912, 1916, 1927, Geijskes 1929). None of these authors mentions the presence of Lobelia dortmanna, which was a rare plant in The Netherlands and certainly would have been noticed if present. Bergmans (1926) recorded Lobelia in small quantities in the Voorste Goorven. Thus the presence of Lobelia in the 15-cm level may indicate that the sediments at this depth were deposited well before ca 1910. This is in good agreement with the time of deposition as obtained from the Pb-210 results (approximately 1884-1900).

Between a sediment depth of 10 to 15 cm an upcore increase in the number of chironomid taxa associated with meso- to polyhumic waters was noted (e.g. Acamptocladius submontanus, Labrundinia longipalpus, Zalutschia sp. and Heterotanytarsus apicalis). This combination of chironomids has never been reported as a living assemblage from The Netherlands. In Sweden this essemblage has been reported for three lakes: Östra Vontjärn (polyhumic), Stråken (mesohumic) and Skärhultsjön (oligohumic) by Brundin (1949). These lakes are oligotrophic, with a pH between 5.8 to 6.8. The diatom inferred pH for the 11-12-cm depth layer (Pb-210 dated at ca 1914-1925) in Achterste Goorven was 5.8 (Fig. 6), in good agreement with the plankton tow inferred pH for the period 1925-1929 (5.7) and the observed pH for the period 1919-1926 (6.0).

Thus the diatoms and chironomid data for Achterste Goorven indicate that the 10-15-cm depth represents the highest pH levels that this pool reached over the last 150 years. In addition, the blue-green alga Gloeotrichia sp. which is typically associated with a pH above 5.5 (Prescott 1962) was found at this depth (Fig. 12).

10-cm to top of core

A substantial increase in the relative number of Chironomus head capsules between 0-10 cm (Fig. 8b) was associated with a concomitant decrease in chironomid species richness. Thus as the pool acidified, its chironomid assemblages species richness declined as taxa associated with disturbed conditions such as Chironomus (Moller Pillot 1984b) replaced many of the pool's previous inhabitants. The dramatic increase in the relative abundance of the acid indicator species Psectrocladius platypus (ibid.) supported the contention that Achterste Goorven has been rapidly acidifying.

It is noteworthy that Walker et al. (1985) observed similar upcore changes in subfossil chironomids in a small humic lake in New Brunswick, Canada. This supports Saether's (1975) contention about the resemblance of palaearctic and nearctic chironomid assemblages.

The most recently deposited sediments which were examined for pollen and algal spores (1-2 cm) contained numerous zygospores of the filamentous green alga Mougeotia spp. Species of this genus have been found to grow prolifically in acidifying lakes, as soon as pH is below 5.5 (Stokes 1981, Schindler et al. 1985). Many Mougeotia species have been reported to exhibit a considerable tolerance to heavy metals (Foster 1982, Francke & Hillebrand 1980). Heavy metal mobilization associated with acid rain is well documented (Tolonen & Jaakkola 1980, Charles 1982, Schindler et al. 1980).

The increase of Urtica (nettles) pollen in the upper sediment samples of Achterste Goorven indicates an extension of nitrogen-rich habitats in the

agricultural area which is situated at a distance of 1-2 km from this moorland pool.

Sediment compaction and mixing

If sediment sampling intervals are short (i.e. 1-2 cm), the trends in all pollen concentration profiles (Fig. 11) can be explained in terms of sediment accumulation rates (Middeldorp 1982, 1984). In the present study, sediment sample distances of 5 cm were adopted for pollen profiling. Although a detailed time scale analysis was not possible, general trends in pollen accumulation rates are evident. These trends indicate that the high pollen concentrations in the intermediate sediment depth layer (5-20 cm) were associated with a well compacted sediment. This is in sharp contrast to the poorly compacted surficial sediments (0-5 cm) where the water content reached 95% (Table 1). Pollen concentrations were also very low in the deepest portion of the Achterste Goorven core (20-34 cm) and this was associated with large quantities of coarse sand (Table 1) which presumably acted as a 'diluting' factor.

As already noted in the results section the Pb-210 activity profile (Fig. 3) indicates some infiltration of surface water into the interstitial waters of the surficial (0-4) sediments. Evidence for vertical mixing of sediments in this layer as well was obtained from the replicate core AG4, which shows constant Pb-210 activity in this surficial layer (Van der Wijk & Mook, in press). Also the comparison of plankton tow diatoms and sediment core diatoms (Fig. 7) indicates mixing of sediment. Although Eunotia exigua, an acidobiontic diatom was absent from the plankton tow samples from the period 1925-1929, it is present with a relative abundance of 1% in the 11-12-cm horizon (Table 3), which was dated by Pb-210 to the same period. Similarly this species has also a higher abundance in the sediments at 6-7 cm than in the plankton tow samples from 1950-1953. The downcore disappearance is more gradual than its disappearance from the plankton tow samples. Also in the relative abundance of other taxa in the plankton tows and the sediments often a discrepancy is found (Fig. 7), although the trends are often the same.

As a result of the mixing of sediments the relative abundance of Eunotia exigua in the surficial sediment layer is lower than expected. Therefore, diatom inferred pH for the surface sediments (4.8) was significantly higher than the observed and plankton tow inferred pH (both 4.2). The sediment core diatom inferred pH at 11-12 cm (5.8) was in accordance with the plankton tow diatom inferred pH for the period 1925-'29 (5.7) and the observed pH in the same period (6.0). Thus the decline of the pH, based on sediment diatom inferred pH (1.0 unit) is much lower than the decline of the pH based on plankton tow diatom inferred pH (1.5 unit) or direct observation (1.8 unit). Therefore, estimates of the rate of acidification from sediment core diatoms will consequently underrate the lake acidification where vertical mixing is indicated.

The fact that the organic sediments of Achterste Goorven are much thicker at wind sheltered than at wind exposed locations indicates that horizontal mixing, i.e. lateral transport of sediment e.g. by wind action, may have taken place as well. This is supported by the Pb-210 measurements, yielding a total integrated activity that is much lower than the average atmospheric Pb-210 fall out in this region (Crozaz et al. 1964, Van der Wijk & Mook, in press). This, and the fact that the Pb-210 activity depth profile shows continuous exponential behaviour may indicate a continuous transport of (suspended) sediment away from the location AG 7. This constant transport

however does not affect the interpretation of the other data.

Below a depth of 12 cm in a profile the sediment diatom inferred pH is lower than at 12 cm. As discussed in the section on historical development of the pool there was a connection more than 100 years ago between the originally oligotrophic (low pH) pool Achterste Goorven and the more mesotrophic (higher pH) pool Voorste Goorven. If the high pH at depths below 12 cm is a result of this connection one would expect the sediment horizon with the highest diatom inferred pH to be at least 100 years old. This is in contradiction with the Pb-210 date of ca 1914-1925 for this horizon. Further studies, e.g. on sediment remains of desmids, of which the living assemblages have been studied by Heimans (1925) and Coesel et al. (1978) may shed light on this question.

SUMMARY

Most palaeolimnological studies have been carried out in relatively deep lakes, where perturbation of the sedimentation process by wind action and bioturbation are of minor importance and where sediments are not exposed to the atmosphere in extremely dry years. The purpose of this study was to investigate the applicability of palaeolimnological methods in a shallow soft water pool in order to determine the rate of acidification.

Pollen stratigraphy provided information about the development of the pool Achterste Goorven over the last 150 years. Pollen and diatom analyses all indicated that our Achterste Goorven sampling site existed as a terrestrial environment shortly after reafforestation with Scots pines of the aeolian drift sands which started in the early 1800s.

The acidification of Achterste Goorven was associated with a decrease in both chironomid and diatom diversity. The chironomid assemblage occurring below 15 cm was relatively diverse and has no living counterpart in The Netherlands. It has been described for poorly buffered waters in Scandinavia. The upcore replacement pattern of chironomid assemblages which took place in Achterste Goorven as it acidified was similar to the one described by Walker et al. (1985) for a small acidifying Canadian lake. Thus the chironomid assemblage from the early 1800s in Achterste Goorven would appear to be amphiatlantic.

The pH inferred from the plankton tow diatoms which were collected from 1925 to 1929 was 5.7. The 11-12 cm deep sediments were dated at 60-70 years of age (Fig. 3). The diatom inferred pH of these 11-12 cm deep sediments was 5.8 (Fig. 6). Achterste Goorven is undergoing rapid acidification. During the last 60 years, sediment core diatom inferred pH has fallen from 5.8 to 4.8, observed pH has fallen from 6 to 4.2 and plankton tow diatom inferred pH has fallen from 5.7 to 4.2. During this same period there was a concomitant increase in the relative abundance of acid tolerant chironomid and diatom species and a concomitant reduction in the relative abundance of acid intolerant chironomid and diatom taxa (Table 2, Fig. 8b).

These data indicate that the rate of acidification in Achterste Goorven is among the highest reported to date. Two major factors are responsible for this high rate of acidification: the small volume of the pool and the high level of wet and dry deposition of acidifying substances in the area. The only water bodies outside the Netherlands of which we are aware that those are acidifying faster than Achterste Goorven are located near Gothenburg, Sweden. Mean pH in these lakes fell from 6.6 to 4.7 during the period 1968-1979 (Morling 1981).

In conclusion, our results indicate that useful stratigraphic information can be obtained from an analysis of the sediments of moorland pools as long

as it is recognized that mixing of microfossils typically occurs to a larger extent in these shallow pools than it does in sediments from deeper bodies of water.

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HOOFDSTUK 6

PALAEOLIMNOLOGICAL AND DOCUMENTED EVIDENCE FOR ALKALIZATION AND ACIDIFICATION OF TWO MOORLAND POOLS (THE NETHERLANDS)

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ABSTRACT

Acidity changes in two isolated perched water moorland pools in The Netherlands were reconstructed from diatoms and cladocerans in sediment cores and interpreted with the help of documentary evidence. Pb-210 dating was compared with alternative methods. Pollen and other micro- and macrofossils were used for dating and to obtain information about the development of vegetation at the study sites.

The pools studied showed considerably larger pH-changes than acidifying European and American lakes. The pH increased from 4-5 in the first half of the 19th century to c. 6 around 1900, due to eutrophication by external sources, and decreased to recent values between 4 and 5, when eutrophication stopped and acid deposition increased.

Documented evidence of human influence upon the study sites, combined with palaeoecological techniques was found to be necessary to obtain proper conclusions with studies on the history of surface water acidification.

1 INTRODUCTION

The biocommunities of isolated moorland pools in The Netherlands, Belgium and Northern Germany have been severely impoverished by acidification since the beginning of this century. This follows from comparisons of recent and old records of aquatic micro- and macrophytes (Coesel et al., 1978; Van Dam et al., 1981; Roelofs, 1983; Van Dam and Beljaars, 1984). Nothing is known about the acidity status of these dilute pools in the period before the turn of the century, with the exception of Achterste Goorven. This now highly acid pool was acid and oligotrophic in the first half of the 19th century and was disturbed by the inflow of eutrophic water, to reach its highest pH in the first half of the 20th century (Dickman et al., in press).

Moorland pools are confined to regions with an Atlantic climate and

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oligotrophic, sandy soils, which were rather unsuitable for intensive agricultural use in the past. After deforestation, before and during mediaeval times, a vegetation developed with Calluna vulgaris and Erica tetralix as dominant plants. Later, the soils were gradually depleted in nutrients by grazing with sheep. Overgrazing caused the development of aeolian drift sands, with a sparse vegetation of Corynephorus canescens and other graminoid pioneers in many heathlands since the Late Middle Ages. After the introduction of fertilizers and the decrease of the wool prices in the late 19th century the sheep farming declined and the majority of the dry heathlands and drift sands were planted with Scots pine (Pinus sylvestris) (Westhoff et al., 1973; De Smidt, 1975).

Many pools developed into bogs after their formation since the late Pleistocene. Information about the digging of peat, as well as the use of the pools for watering and washing of sheep, retting of flax and hemp, and, after eutrophication, also hatching of fish, can be retrieved from old charters (e.g. Posthumus, 1911; Sloet, 1911; De Jonge van Ellemeet, 1917) and has been revealed by archaeological research (Heidinga, 1984).

These activities probably affected the chemistry of the water in the weakly buffered pools, and their documentary evidence should be taken into account when interpreting pH-reconstructions by means of palaeolimnological techniques in the context of acidification studies. Davis and Smol (1986) also stress the need for historical research on changes in land-use near the study sites for a correct interpretation of the coring results.

The objective of this paper is to describe the acidity changes of two isolated moorland pools and to interpret these changes with the help of information from historical sources. As The Netherlands are in the very centre of the acid atmospheric deposition area in Europe, we expect that the process of acidification of these pools started earlier than in lakes in Norway and Scotland, which began to acidify in the second half of the 19th century (EMEP/CCC, 1984; Battarbee and Charles, 1986).

As data from direct measurements of past hydrochemistry are very scarce, diatoms and cladocerans in sediment cores are used to infer historic pH-values (Krause-Dellin and Steinberg, 1984; Battarbee and Charles,1986). Pb-210 dating, which might give erroneous results in highly acid waters (Simola and Liehu, 1985) is compared with alternative methods, including analysis of diatoms, pollen, seeds, cladocerans and old maps, as recommended by Davis and Smol (1986), and Van der Wijk and Mook (in press). Pollen and other botanical micro- and macrofossils are also used to obtain information about the development of local and regional vegetation of the study sites.

2 SITE DESCRIPTION

Two moorland pools, Gerritsfles and Kliplo, in areas with unconsolidated sands and podzols, were selected for this study (Fig.1). The pools have a perched water table and their catchment area is hardly larger than their surface area. Both isolated pools are situated in some of the most remote nature reserves of The Netherlands and have been acidified over the last sixty years. Their environmental setting and the changes of chemistry, macrophyte communities and diatom assemblages, based on historical documents as well as old plankton tow samples back to 1912 have been described in detail by Van Dam (in review).

The clearwater pool Gerritsfles ($5^{o}49'$ E, $52^{o}10'$ N), near Kootwijk, has a surface area of c. 7 ha and a mean depth of 0.7 m. The pH ranged from 3.9 to 5.5 (median 4.3, n=18) from 1970 through 1984. From 1928 through 1930 values between 5.5 and 6.5 were found (n=9).

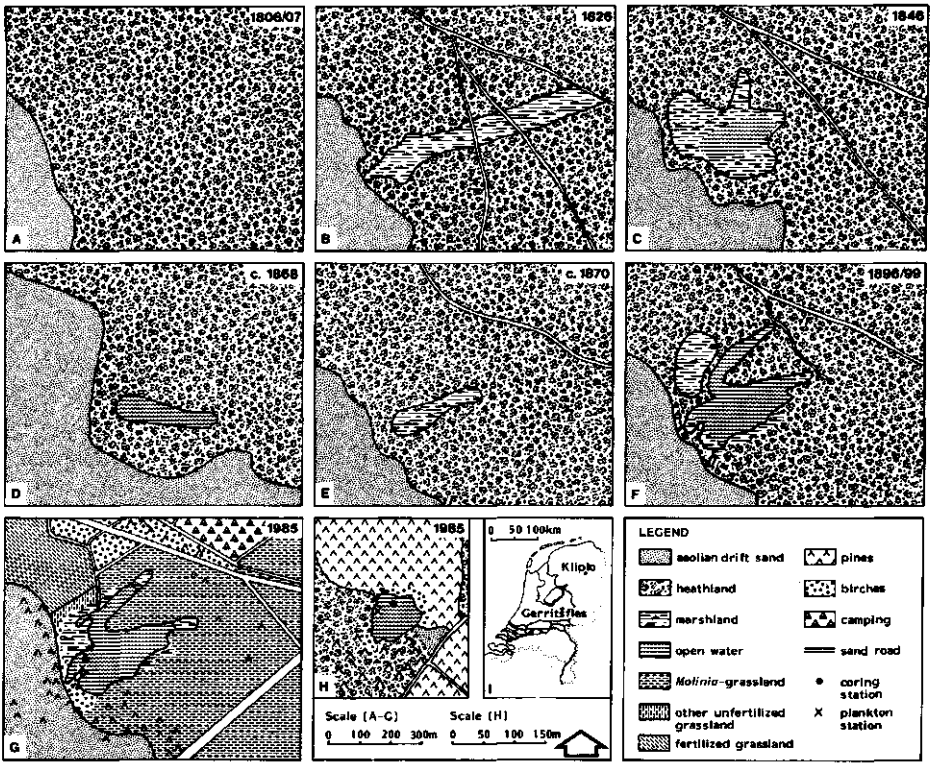


Fig. 1. Historical development of Gerritsfles (A-G), Kliplo (H) and location of pools in The Netherlands (I). References to maps (original scales in brackets): A De Man (1802-1812) (c. 1 : 14400), B Cadastral map (Land Registry Office, Arnhem) (1 : 5000), C Draft of Topographical map of The Netherlands (TMN) (State Archive, The Hague) (1 : 25000), D Map of Municipality of Barneveld (Nairac Museum, Barneveld) (1 : 20000), E TMN (1 : 25000), F Draft of cadastral map (Land Registry Office, Arnhem) (1 : 2500) and TMN (1 : 25000), G,H TMN (1 : 10000) and own survey (1 : 1000).

The brownwater pool Kliplo (6°26' E, 52°50' N), near Dwingeloo, has a surface area of c. 0.6 ha and a mean depth of 0.8 m (Fig.1). The pH ranged from 3.9 to 8.8 (median 5.3, n=34) in the period 1970-1984. From 1924 through 1929 values between 6.0 and 6.5 were found (n=3).

3 MATERIAL AND METHODS

Changes in topography and land-use were studied from published and unpublished maps and other documents.

A core from Gerritsfles was taken on 28-2-1985 from a locality close to the permanent plankton tow monitoring station; Kliplo was cored on 31-1-1985 (Fig.1). Both cores were cut in 1-cm sections in the laboratory within a few hours after sampling. Plankton tow diatoms were obtained from old

collections and from biannually taken samples from 1979 through 1984. Methods for sampling and investigation of diatoms, pollen, seeds and fruits have been described by Dickman et al. (in press).

Van der Wijk and Mook (in press) described the analytical methods used for Pb-210 measurements. The age of the sediments was estimated by the constant rate of supply model (Appleby and Oldfield, 1978). The limits of the age of each 1-cm section are expressed as the Pb-210-inferred age of the base depth of the section plus the one sigma uncertainty, based on nuclear counting statistics and the Pb-210-inferred age of the top depth of the section minus the one sigma uncertainty.

Pollen and other remains of organisms in the pollen slides were counted until c. 300 pollen grains were tallied. The remaining part of the slide was scanned to detect sparsely occurring taxa, which are indicated by a "+" in the diagrams. Pollen diagrams were drawn using a computer program written by Melief and Wijmstra (1984).

Unless indicated otherwise 400 diatom valves were counted in each sample. If valve densities were very low, less valves were counted.

The pH was estimated from the composition of the diatom assemblages by three methods. Index B was calculated according to Renberg and Hellberg (1982). pH_r was calculated from index B, using the relationship given by these authors (st. dev. 0.3). pH_d was calculated using the equation pHd = 5.85-0.54logB (st. dev. 0.8). This equation was obtained by regression of the observed pH of 99 samples from 97 relatively pristine soft water lakes and pools in Denmark, Belgium, The Netherlands, and Germany (Van Dam and Beljaars, 1984). pH_w was calculated by weighted averaging (st. dev. 0.7) (Van Dam, in review). In strongly acid waters ($pH \leq 4.5$) pH_w gives the most accurate results.

Water level changes were inferred from changes in the relative abundance of aerophilous diatoms, which have a pronounced optimum in temporary dry habitats. Indications were borrowed from Beger (1927), Krasske (1936), Hustedt (1942), Sims (1978), Germain (1981) and others.

To detect the remains of cladocerans in the core slices, 4 ml of sediment was taken with a syringe from the fraction 150-500 µm. After dispersion in a sonarbath for 1-3 s the syringe was emptied and rinsed with water above a buoyancy density column (Jacquet et al., 1984). After 10 min the glycerine layer was siphoned off. The ethylglycol and water layers remained in the column. The glycerine layer was checked (x 40 magnification) for the presence of cladoceran remains. Nearly always 80-90% of the remains was retained in the water and ethylglycol layers. Two ml of the residue was placed in a cuvette with 2 ml water and the cladoceran remains were counted under an inverted microscope (x 125-250 magnification). Additionally one or a few drops were examined with a microscope (x 40-400 magnification). Flössner (1972) was used as a taxonomic reference. Valves, headshields and postabdomens were counted as one individual. Approximately 500 remains were counted in each sample.

Plankton tow cladocera were gathered with a net (mesh width 60 µm). As an average 90 or 60 individuals were counted under a microscope (x 40-400 magnification) in each of the 1964-65- and 1983-samples respectively.

Cladocera were classified into each of Hustedt's (1939) pH-groups (acidobiontic, acidophilous, circumneutral, alkaliphilous and alkalibiontic) and a group 'indifferent' for species with a very wide pH-tolerance, using autecological information from the literature (e.g. Luyten, 1934; Klie, 1937; Vallin, 1953; Corijn, 1969; Flössner, 1972; Eie, 1974; Notenboom-Ram, 1981; Krause-Dellin and Steinberg, 1984).

Similarity coefficients were calculated using index SIMI (Johnson and

Millie, 1982), which is particularly sensitive to the contribution of the most common taxa, whose relative abundance could be estimated more reliably than that of rare taxa.

4 RESULTS

4.1 Gerritsfles

4.1.1 Documented changes in topography, land- and water-use

The topographical changes of Gerritsfles and its environment are displayed in Fig.1. In 1806/7 the area of the present pool was depicted as heathland, just east of the bordering dune ridge of the 'Harskamperzand' (including 'Freselsche Zand' or 'Vreesche Zand'), a vast aeolian drift sand area. Bordering dune ridges (with a steep slope at the lee) are formed if the expansion of a drift sand area is hampered, e.g. by humid heathlands (Hesselink, 1920; Koster, 1978). According to descriptions by 'sand inspectors' the surface area of the 'Harskamperzand' would have been fairly stable between c. 1550 and c. 1750. The activity of the sand was particularly high from 1750 to 1830. The surface area of this drift sand increased rapidly from 341 ha in 1810 to 844 ha in 1826, due to the neglect of measurements to control the expansion of the sand during the French occupation (1795-1813). Later on, the area of the sand increased much slower, due to control measurements, e.g. planting of Ammophila arenaria and Scots pines (Sloet, 1852; Hesselink, 1920, 1926; Brandt-Boomstra and Meyman, 1970; Wartena, 1985).

In the 20th century the drift sand has been invaded by Scots pines, which have been planted in the region of the pool since 1850 and particularly after 1898 (Jager Gerlings, 1907; Hesselink, 1920, 1926; Van't Hoff, 1920). The birches (Betula spec.) on the former heathlands are probably seedlings from the belts of birches, which were planted as fire shelters for the pine plantations (Jager Gerlings, 1907; Anonymus, 1920). Calluna vulgaris and Erica tetralix have been outcompeted by Molinia caerulea from the heathlands after 1950 (cf. Schimmel and Mörzer Bruijns, 1952; Stoutjesdijk, 1959).

In the extremely dry year 1826 (Vanderlinden, 1924; Labrijn, 1945) Gerritsfles is represented as a marshy gully, intersected by two tracks.

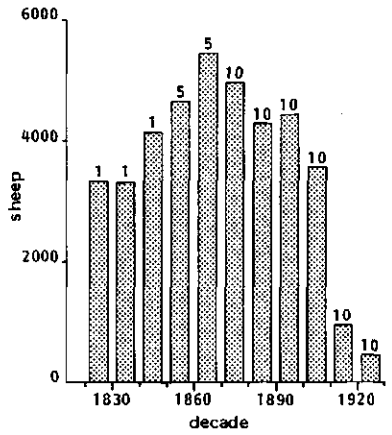


Fig. 2. Average numbers of sheep per decade in the Municipality of Barneveld from 1821 through 1930. Number of observations per decade is indicated at the top of each bar (Anonymus, 1852-1931).

TABLE 1

Percentage abundance of diatoms with a relative abundance ≥1% in at least one sample of the sediments or at least one period of the plankton tow samples in Gerritsfles[a]

			S	E	D	I	N	E	N	T	S	PLANKTON
			Zone 1	Zone 2		Zone 3			Zone 4a		Zone 4b	TOWS
Depth interval of sediment sections (cm)			48 44 39 34	29 26 24 22 19		16 14 12 10			9 6 4		3 2 1 0	16 50 64 77
or period of plankton tow samples (19..)			49 45 40 35	30 27 25 23 20		17 15 13 11			10 7 5		4 3 2 1	18 60 74 84
pH-opt.[b]	R[c]	Taxon[d] Number of samples	1 1[e] 1[e] 1	1 1 1 1 1		1 1 1 1			1 1 1		1 1 1 1	6 5 6 18
3.5	2	Pinnularia subcapitata	9 - 6 -	- 12 - 1 3		1 - - -			- - -		- - - -	- - - -
3.8	1	*Eunotia paludosa	4 - 6 1	- 3 1 2 -		4 + - +			1 - -		- - + -	- - + +
	2	E. denticulata	- - - -	- - - - -		2 - - 1			- - -		- - - -	- + - -
4.0	1	Navicula subtilissima-group	- - - -	2 11 3 24 +		2 7 4 2			3 7 5		1 2 1 1	8 + + +
4.1	1	Eunotia exigua	2 39 1 1	- - 1 - +		3 3 2 2			10 7 11		28 49 50 63	2 6 81 76
	1	Pinnularia subcapitata v. hilseana	- - - 19	- - 2 - 2		- - - -			+ - -		- - - -	- + - -
	1	Neidium densestriatum	- - - -	- - - - 1		- - 2 1			1 1 1		- + 1 -	1 + - +
4.2	1	Frustulia rhomboides v. saxonica	18 2 23 7	7 20 62 60 18		3 9 8 7			10 8		9 9 7 5	8 23 3 11
4.2	2	*Navicula mediocris	- - 1 +	- 4 1 - -		1 - 1 -			- - -		- - - -	- + - -
4.2	2	Eunotia naegelii	1 - 2 -	- 3 + 3 +		3 2 4 3			1 1 3		- 1 1 -	- + - -
4.3	3	E. bilunaris	2 3 1 1	3 4 2 1 1		11 6 1 1			4 10 2		3 1 1 1	30 2 1 +
4.6	3	Pinnularia biceps	- - 2 +	- - - - 1		1 2 1 1			1 2 3		1 2 2 1	1 + - +
4.6	1	Tabellaria quadriseptata	13 1 1 -	3 + 2 - +		7 1 + +			2 1 2		3 3 3 3	1 14 5 7
4.7	2	Frustulia rhomboides	2 - 3 +	- 11 10 3 3		8 + - 2			1 + -		1 - - -	- + - +
4.7	3	Pinnularia absidensis	6 1 - 2	18 2 1 2 3		- - + -			1 1 -		- + + 1	+ - - -
4.8	2	Brachysira brebissonii	- 1 - -	- - - - -		- 2 + -			1 + -		+ - + 1	+ - - -
4.9	2	Eunotia rhomboidea (asym. form)	- - 2 1	3 1 - - 1		9 4 8 2			19 10 15		25 12 16 17	6 29 7 3
5.0	3	Pinnularia microstauron	2 1 - 16	24 4 5 - 8		+ - - 1			- - 1		- + - -	+ 5 1 +
5.0	2	Eunotia incisa	17 5 35 1	1 3 1 - 1		19 19 16 8			34 27 37		15 7 10 4	30 7 1 1
5.0	2	E. rhomboidea (syn. form)	- 1 1 -	6 3 - + -		5 - - 3			- - -		- - 1 1	3 6 1 +
5.0	2	Tabellaria flocculosa	1 - - 1	1 1 1 1 1		5 9 6 7			3 4 3		3 1 1 2	3 3 + +
	2	Eunotia diodon	1 - - +	- - + - 2		1 - - -			- - -		- - - -	- - - -
	2	E. exigua v. meisteri	- - - -	- - - 1 -		- 1 2 -			- 3 4		2 1 1 1	- + - -
5.1	4	Gomphonema parvulum	- 3 - 1	- 1 - - -		- - - -			- - -		- - - -	+ - - -
	2	Stauroneis anceps f. gracilis	- - - -	- + - - +		1 1 1 +			1 1 1		- - - +	+ - - +
	3	Mitzschia gracilis	- - 1 -	- - - - -		1 1 2 2			- 1 -		- 1 - -	+ - - +
5.6	3	Fragilaria virescens	- 1 - -	- - - - -		- - + +			- - 1		- - - -	+ 1 - -
5.6	4	F. construens v. venter	- 1 - -	- - - - -		- - - -			- - -		- - - -	- - - -
	2	Cymbella perpusilla	- - - -	- - - - -		1 - 4 -			2 - -		- - - -	- - - -
	2	Eunotia polydentula	- - - -	- - - - -		2 1 + +			3 1 2		1 1 1 -	+ - - -
	2	E. pectinalis	- - - 7	3 - - + -		+ - - -			- - -		- - - -	- - - -
	3	Gomphonema gracile	- - - -	3 - - - -		- 1 2 3			- - 1		- + 1 -	- - - -
5.9	2	Navicula laptostriata	- - - -	- - - - -		- 2 1 +			- 1 -		+ + - +	+ + - -
5.9	3	Brachysira vitrea f. lanceolata	- - - +	- + + - 3		5 20 13 29			5 9 2		3 3 2 -	4 1 - +
	2	Eunotia elegans	- - - -	- 8 1 - -		1 - - -			- - -		- - - -	+ - - -
	2	Neidium affine v. longiceps	- - - 5	- - - - +		- 1 + -			- 1 1		3 2 2 +	+ 1 - +
6.0	2	Cymbella rabenhorstii	- - - -	- 1 - - +		1 3 1 3			+ 1 -		+ - - -	+ + - -
	2	*Eunotia faliax (incl. v. gracillima)	16 - - 10	7 5 3 3 42		4 1 - 1			1 + -		- - - -	+ - - +
	2	E. glacialis	2 - 5 1	10 4 4 + 8		1 - - -			+ - -		- - - -	- + - -
	-	Achnanthes subsalsa	- - - -	5 - - - -		- - 1 -			- - -		- - - -	- - - -
6.8	3	Achnanthes minutissima	+ 31 - -	- - - - 1		1 3 9 10			- -		1 + - -	+ + + +
	-	Caloneis lauteri	- - - 4	- - - - -		- - - -			- - -		- - - -	- - - -
	3	*Stauroneis obtusa	- - - 12	- - - - -		- - - -			- - -		- - - -	- - - -
	3	*S. borrichii	1 - 2 7	- - - - -		- - - -			- - -		- - - -	- - - -
	3	*Pinnularia borealis	1 - 2 1	- - - - -		- - - -			- - -		- - - -	+ + - -
	3	Mitzschia palea	- 3 - +	- - - - -		- - - -			- - -		1 - - -	- - - -
	3	Navicula seminulum	- 4 - -	- - - - -		- - - -			- - -		- - - -	- - - -
	3	Neidium affine	+ - - -	2 - - - -		- - + -			+ 1 +		- + - 1	+ + + +
	3	N. iridis f. vernalis	1 1 8 3	- - - 1 -		- - - -			- + 1		1 1 1 1	+ - - +
	4	Mitzschia perminuta	- - - -	3 - - - +		+ 1 7 2			1 1 +		- - - -	+ + - +
	4	Brachysira vitrea	- - - -	- - - - -		- 3 1 11			+ + -		1 3 - +	- - - -
	4	Achnanthes austriaca	- - - -	- - - - -		- - 1 -			- - -		- - - -	- - - -
	4	A. austriaca v. helvetica	- - 2 1	1 - - - -		- - 2 -			- - -		- - - -	- - - -
	4	Fragilaria capucina v. vaucheriae	- 2 - -	- - - - -		- - - -			- - -		- - - -	- - - -
	4	Gomphonema angustatum	- 1 - -	- - - - -		- - - -			- - -		- - - -	- - - -
	4	Achnanthes lanceolata	- 1 - -	- - - - -		- - - -			- - -		- - - -	- - - +
Average number of taxa per sample			24 25 21 31	18 26 22 15 26		34 27 38 32			28 30 21		21 25 22 21	17 17 8 8
Average dominance percentage			18 39 35 19	24 20 62 60 18		19 20 16 29			34 27 37		28 49 50 63	44 40 81 76
Percentage abundance of aerophilous taxa			22 1 10 31	8 11 4 5 42		10 2 2 2			2 1 0		0 1 0 0	1 1 1 0
Fraction (%) used for pH calculation of pH_v			77 87 81 31	67 82 89 95 43		85 88 73 75			91 89 90		92 91 95 97	96 98 99 99

[a] + = abundance < 0.5%, - = not present in count, [b] Taxa ordered according to increasing pH-optimum, [c] Hustedt (1939) pH-class (1 acidobiontic, 2 acidophilous, 3 circumneutral, 4 alkaliphilous, 5 alkalibiontic), [d] Aerophilous taxa marked by *, [e] 200 valves counted.

Open water might have been present in 'normal' years. The Gerritsfles is indicated as a marshy depression with some open water in 1846. According to a witness the pool had its present shape in 1868, but desiccated for a considerable part by an extreme drought in this year (Moerman, 1934; Labrijn, 1945). On a sketch map of c. 1868, which is apparently not very accurate, an elongated pool, shorter than the marsh of 1826, is indicated

with the name 'Gardersche Flesch', a synonym of Gerritsfles (Anonymus, c. 1880). In c. 1870 a marsh, with the same shape as the pool in c. 1868 is indicated. In 1896/8 the bordering dune ridge of the drift sand is still at the same place as 80 years before, but the pool has an entirely different shape and is indicated as bog and open water.

Traditionally, sheep grazing was by far the most important means of land management in this area (Roessingh, 1979). The sheep from Kootwijk (including the hamlet Essen) were washed in the pool each year (Anonymus, c. 1880). The small pool at the southwestern side of the main pool (Fig. 1f) was dug as a place for washing sheep, when the bottom of the main pool became too muddy for this purpose (Moerman, 1934). The results of sheep countings in the Municipality of Barneveld between 1820 and 1931 are shown in Fig.2. The numbers of sheep in Kootwijk, in the territory of Barneveld, were not registered separately. In 1888 about 40% of the sheep in Barneveld were from Kootwijk and Garderen (Hartog, 1890). Therefore it is reasonable to assume that c. 20% of the sheep in Barneveld were from Kootwijk (H.K. Roessingh, Wageningen, pers. comm., 1987). Thus c. 1000 to c. 1200 sheep would have been washed in Gerritsfles each year from 1860 through 1900. By the end of the 19th century the number of sheep decreased dramatically (Fig.2).

According to Hesselink (1915) it was possible for the last time in c. 1880 to catch fish by drainage of the pool, after piercing the bordering dune ridge. From c. 1920 through c. 1960 the pool was regularly used for swimming (e.g. Thijsse, 1928; Wigman, 1932).

4.1.2 Similarity analysis

The values for the mean composition of the plankton tow samples are slightly different from those given by Van Dam (in review), because the means were weighted (Table 1). For example, in the period 1977-84 only one sample was taken in 1977 and five samples were taken in 1978. The sample from 1977 was assumed to represent a whole year, while the composition of 1978 was calculated as the average of five samples. Subsequently the average composition for 1977-84 was calculated as the mean of eight yearly values.

The composition of the plankton tow assemblages changed thoroughly between 1960 and 1964 and has remained rather constant since (Table 1). This is reflected by the fossil assemblages. The sediment sections from 6-7, 3-4 and 0-3 cm show very high similarities with the plankton tow samples from the periods 1916-18, 1950-60 and 1964-84 respectively and were presumably deposited in corresponding periods (Table 2). The succession of Eunotia incisa, E. rhomboidea and E. exigua in the plankton tows is neatly reflected in the sediments.

The results of the cladoceran counts are given in Table 3. The samples from 1964-65 show high similarities (>0.84) with the sediment samples from the upper few centimetres (Table 4). Below 2 cm depth the similarity coefficients are lower, but markedly higher than the corresponding similarity coefficients of the diatom assemblages. The few plankton tow samples from 1983 have rather low similarities ($\leq$ 0.57) with the sediment assemblages (Table 4). Some species, notably Diaphanosoma brachyurum, were present in the samples from 1983, but not in the fossil assemblages. If these species are omitted from the calculations the similarities between the plankton and sediment assemblages are higher and the 1983-samples are most similar to the 1-2-cm sample (Table 4). The cladocerans indicate that the topmost 4 cm would have been deposited since c. 1960.

The agreement between Pb-210-dating (Table 5) and biological dating is fair.

TABLE 2

Similarity indices (SIMI) between plankton tow and sediment core diatom assemblages in Gerritsfles

Depth (cm)/ Period	1916 1918	1950 1960	1964 1974	1977 1984
0-1	.14	.38	.98	.97
1-2	.25	.46	.95	.95
2-3	.21	.43	.96	.97
3-4	.44	.72	.73	.72
4-5	.73	.55	.30	.30
6-7	.87	.55	.25	.26
9-10	.75	.61	.29	.28
10-11	.32	.24	.06	.08
12-13	.60	.49	.10	.12
14-15	.69	.39	.10	.13
16-17	.82	.54	.14	.14
19-20	.12	.25	.02	.06
22-23	.25	.52	.03	.13
24-25	.21	.57	.05	.16
26-27	.35	.45	.03	.10
29-30	.15	.31	.03	.04
34-35	.07	.20	.03	.05
39-40	.65	.46	.05	.11
44-45	.14	.15	.77	.76
48-49	.48	.52	.10	.17
1977-84	.08	.27	.99	1.00
1964-74	.08	.23	1.00	.99
1950-60	.38	1.00	.23	.27
1916-18	1.00	.38	.08	.08

TABLE 4

Similarity indices (SIMI) between plankton tow and sediment core cladoceran assemblages in Gerritsfles

Depth (cm)/ Period	All taxa 1964 1965	All taxa 1983	Exclusively planktonic taxa excluded 1964 1965	Exclusively planktonic taxa excluded 1983
0-1	.90	.47	.90	.66
1-2	.84	.57	.84	.81
2-3	.75	.53	.75	.74
3-4	.76	.52	.76	.72
4-5	.67	.47	.67	.65
6-7	.55	.35	.55	.60
8-9	.50	.42	.50	.59
10-11	.55	.32	.55	.45
11-12	.67	.42	.67	.60
12-13	.57	.39	.57	.54
14-15	.53	.37	.53	.52
19-20	.73	.35	.73	.48
24-25	.75	.41	.76	.58
29-30	.41	.20	.41	.29
48-49	.74	.33	.74	.46
1983	.56	1.00	.78	1.00
1964-65	1.00	.56	1.00	.78

TABLE 3

Percentage abundance of taxa and pH-groups of cladocerans in Gerritsfles[a]

	S	E	D	I	M	E	N	T	S				PLANKTON TOWS	
	Zone 1			Zone 2			Zone 3			Zone 4a			Zone 4b					
Depth interval (cm) or period	48 49	44 45	39 40	34 35	29 30	24 25	19 20	14 15	12 13	11 12	10 11	8 9	6 7	4 5	3 4	2 3	1 2	0 1	1964 1965	1983 1983
Number of samples	1	1[b]	1[b]	1[b]	1	1	1	1	1	1	1	1	1	1	1	1	1	1	10	3
Individuals counted	158	-	-	-	138	401	100	351	361	358	488	382	519	358	544	100	374	274	576	508
Acantholeberis curvirostris	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	2	-	-	4	3
Alonella excisa	7	-	-	-	-	14	6	7	6	8	13	3	5	8	11	8	17	23	36	19
Bosmina longispina	-	-	-	-	1	5	2	10	12	11	4	18	9	13	15	16	18	6	9	26
Subtotals acidobiontic taxa	7	-	-	-	1	19	8	17	18	17	17	21	14	21	26	26	35	29	49	48
Alonella nana	1	-	-	-	7	8	1	9	6	1	15	3	4	4	2	5	1	-	1	-
Eurycercus glacialis	-	-	-	-	-	-	-	1	-	-	+	+	+	+	+	1	-	-	-	-
Subtotals acidophilous taxa	1	-	-	-	7	8	1	10	6	1	15	3	4	4	2	6	1	-	1	-
Acroperus elongatus	-	-	-	-	-	-	-	1	-	-	-	1	1	1	+	+	+	-	+	-
Acroperus harpae	-	-	-	-	2	6	2	23	3	11	13	15	22	17	14	9	7	2	-	-
Alona affinis	1	-	-	-	29	23	17	15	32	25	25	26	21	14	15	11	16	10	-	1
Alona guttata	1	-	-	-	29	3	8	1	2	4	8	4	4	4	3	4	2	+	1	-
Alona rectangula	-	-	-	+	1	4	2	1	4	-	1	2	3	2	3	3	2	-	+	-
Alonella exigua	-	-	-	-	-	+	-	-	-	-	-	-	+	3	1	-	1	-	9	-
Camptocercus rectirostris	-	-	-	-	2	1	5	3	1	3	2	2	3	5	2	3	1	+	+	-
Ceriodaphnia quadrangula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	+
Diaphanosoma brachyurum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	35
Graptoleberis testudinaria	1	-	-	-	-	2	2	7	2	2	2	3	2	5	2	6	1	2	-	-
Monospilus dispar	-	-	-	-	-	+	1	3	3	1	1	-	-	-	-	-	-	+	-	-
Scapholeberis mucronata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Subtotals circumneutral taxa	3	-	-	-	63	39	36	54	47	46	51	53	56	51	40	36	30	14	13	36
Chydorus sphaericus	89	+	+	+	29	34	55	19	29	34	17	23	26	25	31	32	35	56	37	15
Subtotals indifferent taxa	89	-	-	-	29	34	55	19	29	34	17	23	26	25	31	32	35	56	37	15
Number of taxa	6	1	1	2	8	13	11	13	11	10	10	12	13	14	13	13	12	10	12	7

[a] + = taxon present (abundance < 0.5%), - = taxon not found, [b] number of cladoceran rests extremely low; no quantitative estimation possible.

TABLE 5

Physical characteristics and Pb-210 dating of Gerritsfles sediment core

Depth (cm)	Water (%)	Inorganic matter (%)	Organic matter (%)	Year AD
0-1	71.5	21.8	6.7	1979-1985
1-2	-	-	-	1972-1979
2-3	74.0	19.7	6.3	1966-1973
3-4	75.3	18.1	6.6	1961-1967
4-5	79.4	15.3	5.3	1956-1962
6-7	68.2	25.4	6.4	1928-1949
9-10	58.3	36.9	4.8	1864-1927
14-15	27.3	70.2	2.5	<1830
19-20	35.7	57.7	6.6	<1830
24-25	30.9	64.3	4.8	<1830
29-30	26.6	70.0	3.4	<1830
39-40	17.0	81.4	1.6	<1830

4.1.3 Reconstruction of past environmental setting and biocommunities

Zone 1 (49 to 34 cm)

The very sandy sediment (Table 5) is poor in pollen of hydrophytes and diatom valves. This indicates a high deposition rate of sand, blown in by the wind. The pollen assemblage is indicative of an open landscape, dominated by herbaceous plants with Ericaceae and wild grasses (Figs.3 and 4). Considering the records of seeds, Erica tetralix was present at the site, but Calluna vulgaris was probably responsible for the dominance of Ericaceae pollen in this zone and the next one. C. vulgaris is zoogamous, but releases great quantities of pollen into the air at the end of the flowering season (Faegri and Iversen, 1975). Pollen and macrofossils (Figs.4, 5 and 6) reflect that the coring site was in a shallow puddle of a humid heath with Erica tetralix, Juncus spec. and Succisa pratensis. Botryococcus, Zygnema type and some pollen of the amphibious Littorella uniflora indicate the temporarily aquatic character of the site.

This is corroborated by the regular presence of aerophilous diatoms. Indicators for pollution by easily degradable organic material, like Gomphonema parvulum, Nitzschia palea and Navicula seminulum (e.g. Cholnoky, 1968) have a relative abundance of 10% at 44-45 cm depth (Table 1). The diatom-inferred pH is approximately 5 (Fig.7).

At the base of the core the eurytopic Chydorus sphaericus dominates and only a few other cladoceran species are present. In the other samples from this zone the cladocerans occurred only erratically, indicating an unsuitable environment for the development of cladocerans, e.g. a very sandy sediment, combined with regular desiccation and shortness of food (Table 3).

The presence of pollen of the cornflower (Centaurea cyanus) and buckwheat (Fagopyrum esculentum), even in the deepest samples, indicates that the sediments were deposited in late- or post mediaeval times (Slicher van Bath, 1964; Roessingh, 1979). This zone might correspond with the topographical situation at the beginning of the 19th century (Fig.1 a), in accordance with the Pb-210 dating (Table 5).

Zone 2 (30 to 19 cm)

The sand content decreases from 70 to 58% in this zone (Table 5). The pollen percentage of Littorella uniflora follows this decrease (Fig.5). Some

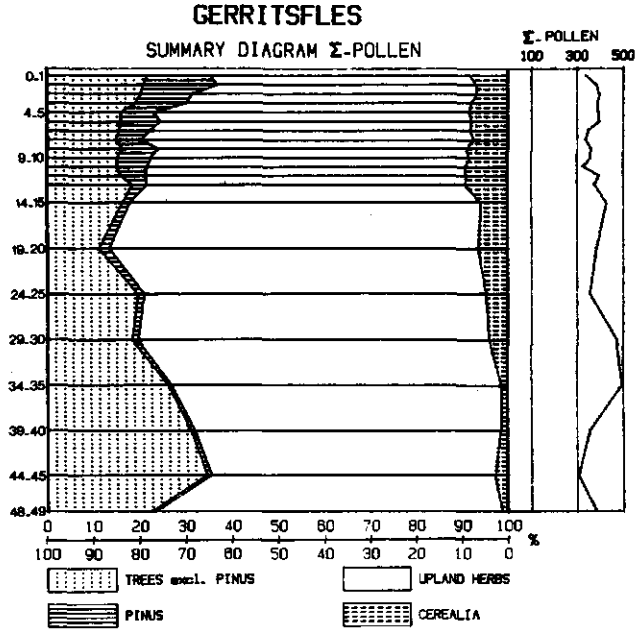


Fig. 3. Iversen diagram (Gerritsfles).

seeds of this species were seen at 29-30 cm (Fig.6). Spores of Mougeotia (often found in acid waters) and Cyperaceae pollen are at maximum at 25-29 cm. This peak is related to the occurrence of seeds of Eleocharis multicaulis, a member of the Littorellion alliance (Fig.6). The seeds of Körber-Grohne's (1964) Juncus articulatus type, which were very abundant in this zone, include J. bulbosus, belonging to the same alliance. Erica tetralix, Hydrocotyle vulgaris and some Sphagnum sp. were also present in the swampy habitat. H. vulgaris is often found in slightly disturbed (e.g. eutrophied) originally oligotrophic environments. Type 160 has a pronounced maximum in this zone (Fig.5). It was recorded for the first time in a comparable habitat at the base of the raised bog 'Fochtelooërveen' (Klaver, 1981).

The diatom-inferred pH decreases gradually from c. 5 to c. 4 between 30 and 22 cm depth (Fig.7). This is concluded from the increase of Frustulia rhomboides var. saxonica, which is particularly abundant in humic acid waters (Jørgensen, 1948; Niessen, 1956; Germain, 1981) (Table 1). The water might have turned humic because of accumulation of organic material (Table 5). The 19-20-cm sample has a higher diatom-inferred pH (c. 5). Eunotia fallax (including var. gracillima), which is often found on flushing rock surfaces and oligotrophic marshes in Scandinavia, reaches its maximum here. The presence of this diatom and other aerophilous taxa (Table 1) indicates that at least parts of the Gerritsfles desiccated regularly at that time. However, more or less permanently submerged areas must have been present, because otherwise the organic material in the sediment would have been oxidized.

The changes in the pH spectra of the cladocerans parallel the changes of

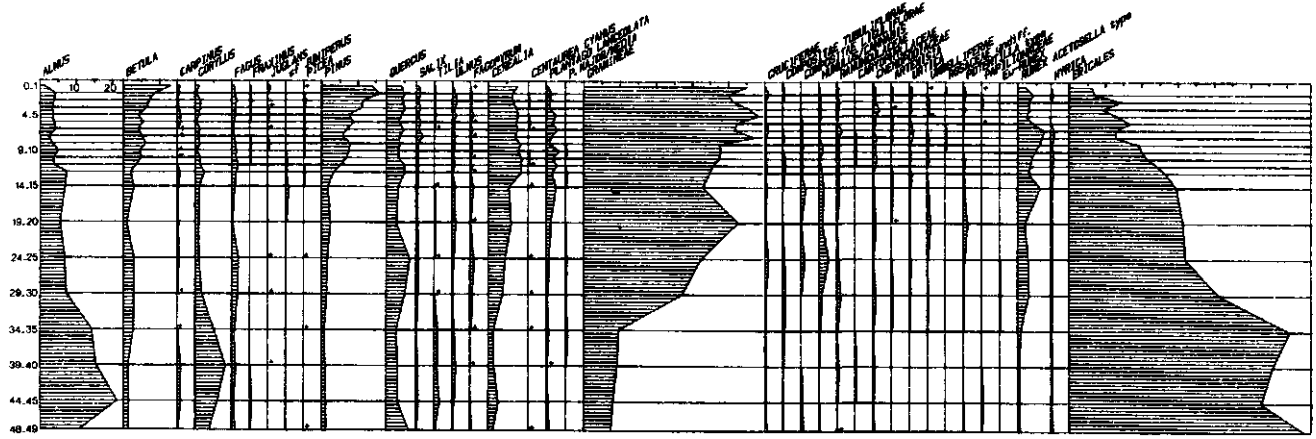
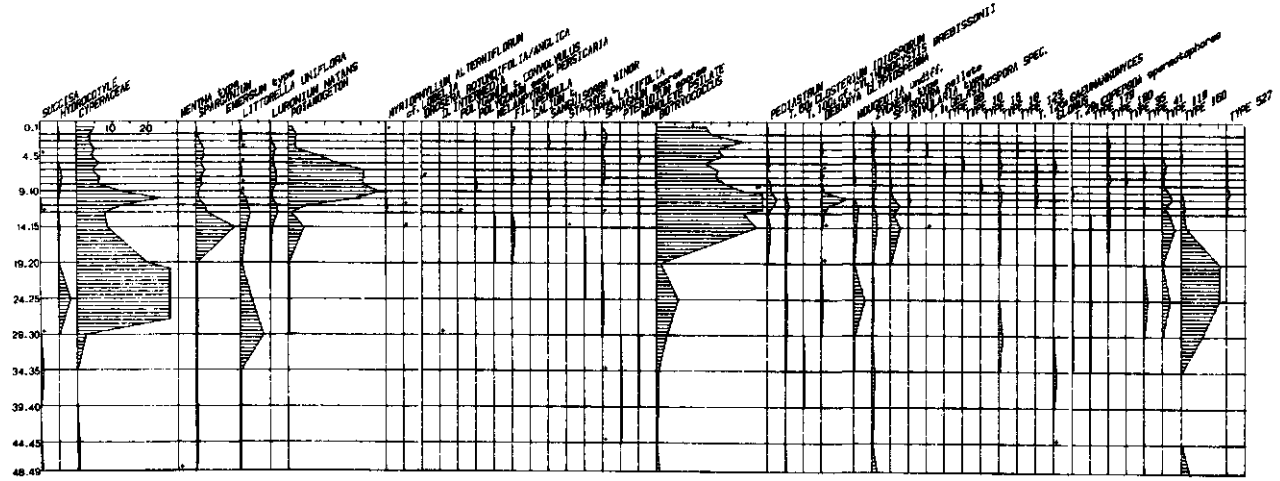


Fig. 4. Σ-pollen: trees and upland herbs (Gerritsfles).


SALIX
HYDROCOTYLE
CYPERACEAE
MENTHA SORTUM
SPARGANIUM
EMERSUM type
LITTORELLA UNIFLORA
LUDWIGIA PALUSTRIS
NUPHAR
HYDROPHYLLUM ALTERNIFOLIUM
CF. UMBELLATA ROTUNDIFOLIA-ANGLICA
TYPE
TYPE
TYPE

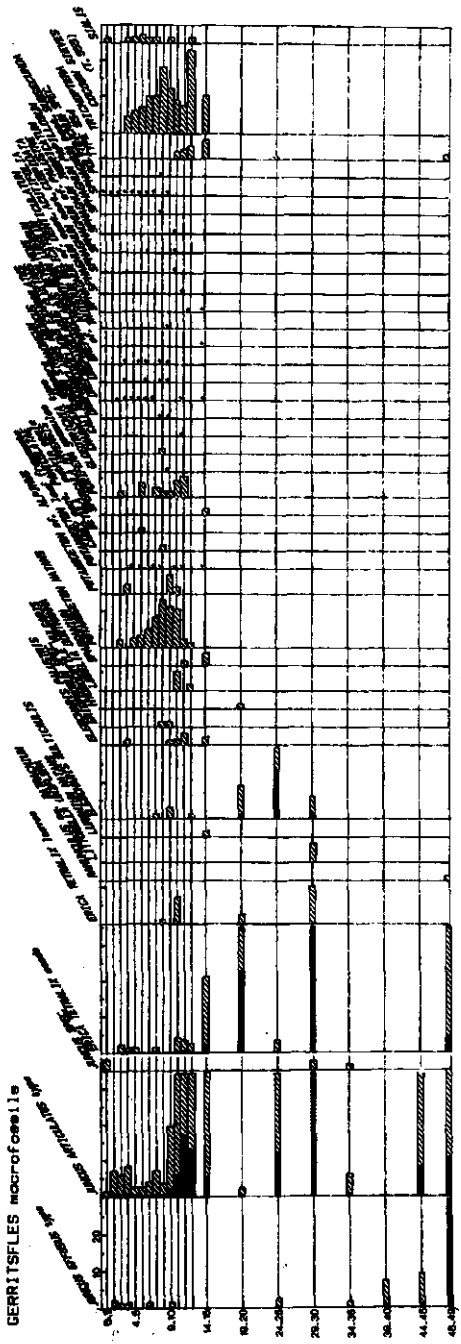


Fig. 6. Fruits, seeds and other macrofossils. Black and hatched parts of the bars represent 1/10 and 1/1 of the indicated scale respectively (Gerritsfles).

the diatom-inferred pH (Figs.7 and 8). The relatively high number of taxa (11-13) in the 19-25-cm depth interval (Table 3) might indicate more favourable conditions than in the preceding zone.

Presumably this zone corresponds with the topographic situation between 1826 and c. 1850 (Fig.1), in agreement with the Pb-210 dating (Table 5). If so, the sedimentation rate would be 3-4 mm per year.

Zone 3 (17-10 cm)

The proportion of sand in this zone decreases from 70 to 37% (Table 5), parallel with an increase of Pinus pollen (Figs. 3 and 4). Presumably the plantation of pines caused a decline of aeolian erosion processes in the area and as a consequence less sand was transported to and deposited in the pool.

Pollen of Littorella, mainly confined to sandy bottoms, is still fairly abundant in the 12-13-cm stratum, but is rare in shallower samples (Fig.5). Seeds of Lobelia dortmanna, also characteristic of sandy substrates, were found in this zone (Fig.6). The local vegetation became more diverse with Sparganium minimum type (probably S. angustifolium, which was still present with sterile forms in 1984) and Luronium natans. Potamogeton natans shows a sharp increase in the upper part of this zone. The increase of these taxa, particularly the latter one, is indicative for moderate eutrophication and a more organic substrate. Also the settlement of Eleocharis palustris and Potamogeton cf. alpinus could be attributed to eutrophication. Sparganium angustifolium and both Potamogeton species do not

withstand frequent desiccation.

In contrast, spores of the rare zygnemataceous alga Debarya glyptosperma are found in temporarily dry environments, indicating the varied habitats present at the Gerritsfles at that time (Fig.5). D. glyptosperma has been found at sites being in a transitional phase from oligotrophic to mesotrophic conditions, due to slight pollution (Ellis-Adam and Van Geel, 1978). Type 555 sieve-like membranes of pupal cases of caddis flies occur abundantly both in this and the next zone (Fig.6). Also some Trichoptera cases are present, presumably belonging to larvae of species from meso-eutrophic waters (L.W.G. Higler, Leersum, pers. comm., 1987). The peak of the alga Botryococcus and the presence of Pediastrum in this zone indicate also more eutrophic conditions than in the preceding zone. The non-diatomaceous algae and higher plants indicate a pH between 5 and 6 in

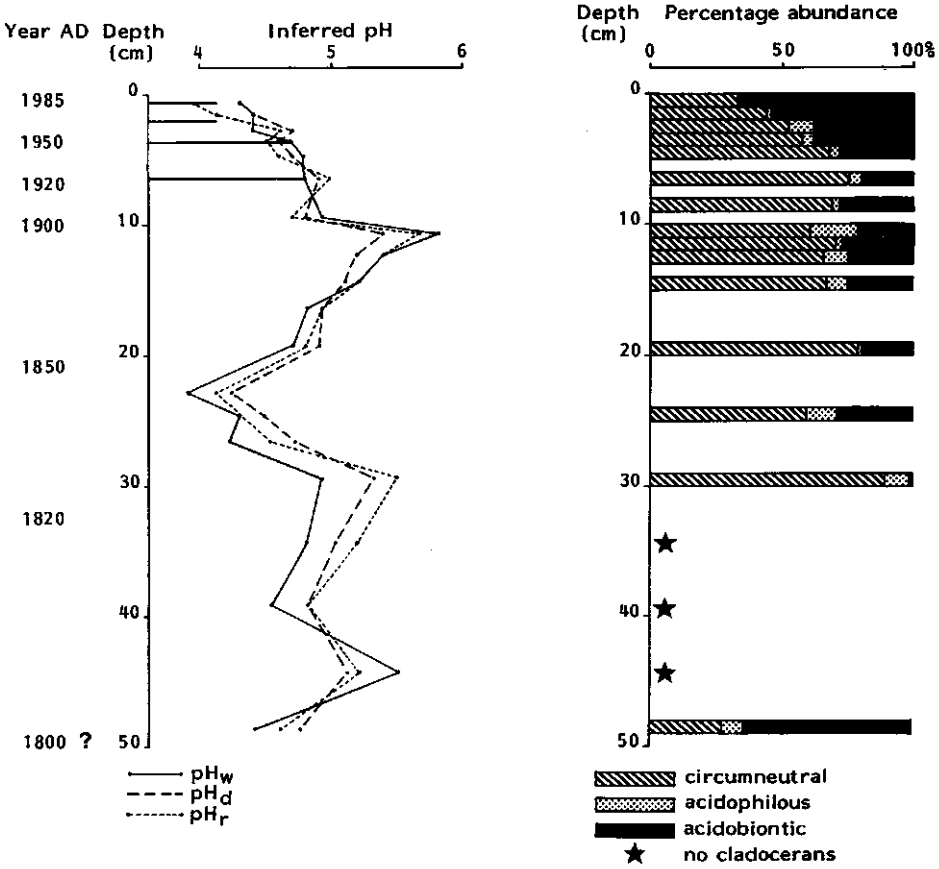


Fig. 7 (left). Diatom-inferred pH in relation to depth. Plankton tow diatom-inferred pH indicated by horizontal bars (Gerritsfles). Dating: 0-7 cm with Pb-210, rest with alternative methods.

Fig. 8 (right). Percentage abundance of cladoceran pH classes, excluding indifferent taxa (Gerritsfles).

this zone. The increase of pH is confirmed by the presence of spiculae of sponges (Jewell, 1939; Tillman and Reiswig, 1982) (Fig.6).

The diatom-inferred pH increases steadily in this part of the profile and attains its maximum value (c. 5.8) at a depth of 10-11 cm. This is concluded from the rise of the weakly acidophilous to alkaliphilous and more or less mesotraphent taxa Brachysira vitrea (including f. lanceolata), Achnanthes minutissima and Nitzschia perminuta. Above 15 cm depth the abundance of aerophilous taxa is low (2%), pointing to permanent aquatic conditions. The heterogeneous environment permits a relatively high number of taxa to coexist (Table 1) (e.g. Smith, 1972).

The increase of pH is not reflected by the cladocerans (Fig.8). The species composition of the cladoceran assemblage is rather similar to that of the preceding zone, but for Eurycercus glacialis, a rare species, indicative for periodically desiccating oligotrophic dune slacks and moorland pools. Monospilus dispar, rather typical for this zone, is rare and confined to sandy bottoms of eutrophic lakes and pools (Frey, 1975; Whiteside, 1970; Notenboom-Ram, 1981).

This zone might correspond with the topographical situation between c. 1850 and 1900 (Fig.1), as water is permanently present and the pines started to increase (Figs.3 and 4). In this case the annual sedimentation rate would be about 1.5 mm. With Pb-210 the base of this zone is dated a few decades too old (Fig.1). As Lobelia dortmanna has been seen for the last time in 1927 (Schimmel and Mörzer Bruijns, 1952) and its seeds were found at a depth of 10-11 cm (Fig. 6), we concluded that the sediments at this depth were deposited prior to 1927, in agreement with Pb-210 dating. The Pb-210-inferred date of the top of this zone is in excellent agreement with the biological data.

Zone 4a (10-4 cm)

The continued plantation of pines and the termination of sheep farming in the region of the pool inhibited wind erosion, leading to a decreased accumulation of sand in the sediments. The sediment became more organic (Table 5) and Littorella uniflora and Lobelia dortmanna disappeared (Figs.5 and 6). Sialis-larvae, preferring an organic bottom, are frequent in this zone (Fig.6). The strong decreases in the pollen percentage and the number of seeds of Potamogeton natans and possibly the decline of Botryococcus are associated with oligotrophication (Figs.5 and 6).

The diatoms indicate a decline of the pH from 5.8 in the 10-11-cm layer to 4.8 in the 4-5-cm layer (Fig.7). The acidophilous Eunotia incisa has its maximum occurrence in this zone. E. rhomboidea and E. exigua are more abundant than in the previous zones. The lower number of taxa compared to zone 3 points to a less heterogeneous environment (Table 1).

The cladoceran pH spectrum does not indicate a change of the pH. The taxonomic composition of the cladoceran assemblage is similar to that in zone 3 (Table 3).

This zone might correspond with the topographical situation from ca 1900 to c. 1945 (Fig.1). If so, the average annual sedimentation rate would be approximately 1.3 mm. The Pb-210 dating of the base of the zone agrees with these results, but with Pb-210 the top is dated 1-2 decades younger than with alternative methods (Table 5).

Zone 4b (4-0 cm)

The sediments are rich in organic matter (Table 5). The decline of the seeds of Potamogeton natans continues (Fig.6). The pollen percentage of this species and that of Sparganium cf. angustifolium decreases strongly (Fig.5). In the upper macrofossil samples only Sphagnum leaves and Juncus seeds are recorded.

The diatoms indicate a further decrease of the pH; from c. 4.6 at 3-4 cm to 4.3 in the top of the core (Fig.7). Eunotia exigua dominates the assemblages and the number of taxa is lower than in the zones 3 and 4a (Table 1).

The cladoceran pH spectrum shows a sharp rise of acidobiontic species (Fig.8), mainly due to the increase of Alonella excisa and the decrease of Acroperus harpae.

As assessed from biological data this zone was deposited from c. 1945 to 1985; consequently the annual sedimentation rate is 1.0 mm.

4.2 Kliplo

4.2.1 Documented changes in topography, land- and water-use

Kliplo and nearby small pools are not well represented on the topographical maps of this region, surveyed between 1811 and 1929. On the map of Beijerinck (1924) and topographical maps after 1936 the pool has approximately its present shape and area (Fig.1).

The pool was probably formed during the transition of the Subboreal to the Subatlantic, in a forested landscape, and developed into a bog. The bottom is sealed by an impervious layer, which developed as a podzol B horizon. Originally the pool was situated in a depression in the landscape. In early mediaeval times the human population expanded and the forests were transformed into heathlands. After overgrazing by sheep large drift sand areas were formed. Probably the 'Lheebroekerzand', where Kliplo is situated, was formed in the Late Middle Ages. The relief has been partially inverted due to wind erosion and at present the water level in Kliplo is higher than the pine forest floor some tens of metres north of the pool. The open water was formed when the peat was excavated for use as fuel. Kliplo was surrounded by vast areas of aeolian drift sand and small patches of heathland until 1890, when the sheep flock of Lheebroek was dissolved. The drift sands were planted and invaded by conifers (mainly Scots pines) on a small scale since 1875 and more intensively since 1906 (Blokhuis, 1935; Jansen, 1946; Schelling, 1955; Vrielink et al., 1976; Booij and Van Oosten, 1978; Kalb, 1984; Bakker et al., 1986).

Tourists used the pool as a bathing place, at least from 1939 until 1971 (Brouwer, 1968; P. Kerssies, pers. comm., 1984).

4.2.2 Similarity analysis

The results of the diatom counts are given in Table 6; the similarities between the plankton tow samples and core assemblages in Table 7. The 1978-84 samples show best similarity (0.84) with the surface sediment assemblages, due to the relatively high proportion of Frustulia rhomboides var. saxonica in these samples. The similarities of the 1978-84 samples are decreasing to 0.07 to a depth of 14-15 cm, but are increasing further to the base of the core, parallel to the increase of Frustulia rhomboides var. saxonica. The similarities of the plankton tow samples from 1948-64 and

TABLE 6

Percentage abundance of diatoms with a relative abundance ≥1% in at least one sample of the sediments or at least one period of the plankton tow samples in Kliplo[a].

			S	E	D	I	M	E	N	T	S	PLANKTON TOWS		
Depth interval of sediment sections (cm)			32	29	24	19	14	9	4	0		24	48	78
or period of plankton tow samples (19..)			33	30	25	20	15	10	5	1		29	64	84
pH-opt.	[b]R	[c] Taxon[d] Number of samples	1[e]	1[f]	1[g]	1	1	1	1	1		2	4	10
3.5	2	Pinnularia subcapitata	-	-	2	+	+	-	-	-		-	-	-
3.8	1	*Eunotia paludosa	6	21	6	-	-	+	-	-		-	+	+
4.0	1	Navicula subtilissima-group	2	1	-	6	-	2	7	9		8	3	18
4.1	1	Eunotia exigua	-	5	6	-	-	-	-	-		-	1	1
	2	Pinnularia spec.	-	-	6	-	-	-	-	-		-	-	-
	1	P. subcapitata var. hilseana	4	3	-	+	-	-	-	-		-	-	-
4.2	1	Frust. rhomboides v. saxonica	42	51	20	4	1	9	11	25		10	8	25
4.2	2	E. naegelii	-	1	-	4	-	1	3	1		-	-	-
	1	*Navicula festiva	4	1	1	1	+	-	-	-		-	-	-
4.3	3	Eunotia bilunaris	4	5	-	10	+	2	1	2		15	10	7
	1	Navicula 'hoefleri'[h]	-	-	-	10	-	1	2	4		3	+	3
	2	Eunotia polydentula	-	-	-	-	-	-	2	1		1	+	+
4.6	3	Pinnularia biceps	-	-	-	+	-	-	3	3		-	+	1
4.6	1	Tabellaria quadriseptata	2	-	4	15	1	2	3	3		4	1	1
4.7	2	Frustulia rhomboides	-	3	-	-	-	-	-	-		-	-	+
4.7	3	Pinnularia abaujensis	12	1	-	1	-	+	+	-		-	+	+
4.9	2	Eunotia rhomboidea (asymm. f.)	-	1	-	+	2	4	5	8		4	3	14
4.9	2	*Pinnularia irrorata	4	2	35	+	-	-	-	-		-	-	-
5.0	2	Eunotia incisa	2	-	2	35	2	2	10	5		16	9	7
5.0	3	Pinnularia microstauron	4	1	4	-	6	7	+	-		-	+	+
5.0	2	Eunotia rhomboidea (symm. f.)	2	-	-	-	1	4	2	2		1	1	1
5.0	2	Tabellaria flocculosa	-	-	-	3	-	4	5	6		24	9	7
5.1	4	Gomphonema parvulum	2	-	-	-	1	-	-	-		1	+	+
	2	Stauroneis anceps f. gracilis	-	-	-	-	-	+	2	1		-	1	+
5.6	3	Fragilaria virescens (incl. vars)	-	-	-	-	41	18	3	4		+	3	1
	3	Gomphonema gracile	-	-	-	5	18	2	-	+		-	+	-
	2	Eunotia pectinalis var. minor	-	1	-	1	6	1	1	-		-	-	-
	2	E. pectinalis (incl. other var.)	-	-	-	-	2	-	1	-		-	-	-
	3	Nitzschia acidoclinata	-	-	1	-	-	3	-	-		-	-	-
5.9	2	Navicula leptostriata	-	-	-	-	-	3	29	17		11	14	7
5.9	3	Brachysira vitrea f. lanceolata	-	-	-	-	-	3	3	5		1	26	3
	2	Cymbella rabenhorstii	-	-	-	-	-	20	3	1		1	2	+
	2	*Eunotia fallax	2	2	-	1	1	-	-	-		-	-	-
	3	Pinnularia viridis	-	1	9	-	-	-	-	+		-	-	-
	3	*P. borealis	-	-	1	+	+	-	-	-		-	+	+
	3	*Navicula fossalis	-	-	3	-	-	+	-	-		-	-	-
	3	Nitzschia gracilis	-	-	-	-	-	-	1	2		-	6	2
	3	*Hantzschia amphioxys	2	-	1	-	-	-	-	+		-	-	-
6.8	3	Achnanthes minutissima	-	-	-	4	15	2	-	-		1	1	+
	4	Nitzschia perminuta	-	-	-	1	1	5	-	-		-	-	-
	4	Brachysira vitrea	-	-	-	+	-	6	5	1		+	+	+
	4	Navicula minima	-	-	1	-	-	-	-	-		-	-	-
	4	Fragilaria capucina	-	-	-	-	2	-	+	-		-	+	-
	5	Cymatosira belgica	2	-	-	-	-	-	-	-		-	-	-
	5	*Rhaphoneis amphiceros	2	-	-	-	-	-	-	-		-	-	-
	5	*Rhaphoneis surirella	2	-	-	-	-	-	-	-		-	-	-
Average number of taxa per sample			18	16	20	26	25	30	27	24		16	21	17
Average dominance percentage			42	51	35	35	30	20	29	25		27	31	35
Percentage abundance of aerophilous taxa			22	26	46	2	2	1	0	1		0	0	0
Fraction (%) used for calculation of pH_w			82	92	77	81	69	62	84	89		95	89	94

[a] + = abundance < 0.5% - = not present in count. [b] Taxa ordered according to increasing pH-optimum, [c] Hustedt (1939) pH-class (1 acidobiontic, 2 acidophilous, 3 circumneutral, 4 alkaliphilous, 5 alkalibiontic), [d] Aerophilous taxa marked by *, [e] 50 valves counted, [f] 100 valves counted, [g] 200 valves counted, [h] sensu Ross and Sims (1978).

1924-29 show the same general pattern, but there are remarkable discontinuities at the 14-15, 19-20 and 24-25-cm depth levels, caused by the casual dominance of Gomphonema gracile, Eunotia incisa and Pinnularia irrorata in these samples. The plankton tow samples of the two earliest periods show highest similarities with the two topmost sediment samples.

4.2.3 Reconstruction of past environmental setting and biocommunities

Zone 1 (33-24 cm)

The sediment is rich in organic matter (Table 8), consisting of fairly well decomposed Ericaceae-Sphagnum peat. The pollen spectra (Figs.9, 10 and 11) are dominated by tree pollen. Ericaceae are excluded from the pollen sum

TABLE 7

Similarity indices (SIMI) between plankton tow and sediment core diatom assemblages in Kliplo

Depth (cm)/ Period	1924 1929	1948 1964	1978 1984
0-1	.63	.60	.89
4-5	.62	.60	.62
9-10	.29	.32	.36
14-15	.04	.10	.07
19-20	.62	.35	.37
24-25	.16	.12	.32
29-30	.29	.23	.64
32-33	.32	.24	.66
1978-84	.67	.53	1.00
1948-64	.60	1.00	.53
1924-29	1.00	.60	.67

TABLE 8

Physical characteristics and Pb-210 dating of Kliplo sediment core

Depth (cm)	Water (%)	Inorganic matter (%)	Organic matter (%)	Year AD
0-1	96.1	1.9	2.0	1983-1985
1-2	90.8	5.0	4.2	1978-1983
2-3	90.3	6.3	3.4	1975-1979
3-4	88.5	10.6	0.9	1971-1975
4-5	83.0	13.2	3.8	1966-1971
6-7	81.9	13.1	5.0	1957-1962
9-10	64.5	29.3	6.2	1942-1948
14-15	33.5	62.2	4.3	1918-1923
19-20	33.1	63.1	3.8	1900-1907
24-25	73.5	7.9	29.9	1878-1886
29-30	72.8	13.2	14.0	1845-1859
32-33	82.0	0.9	17.1	<1830

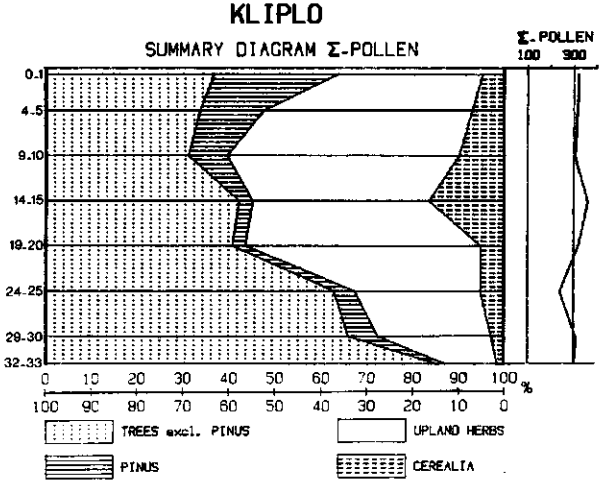


Fig. 9. Iversen diagram (Kliplo).

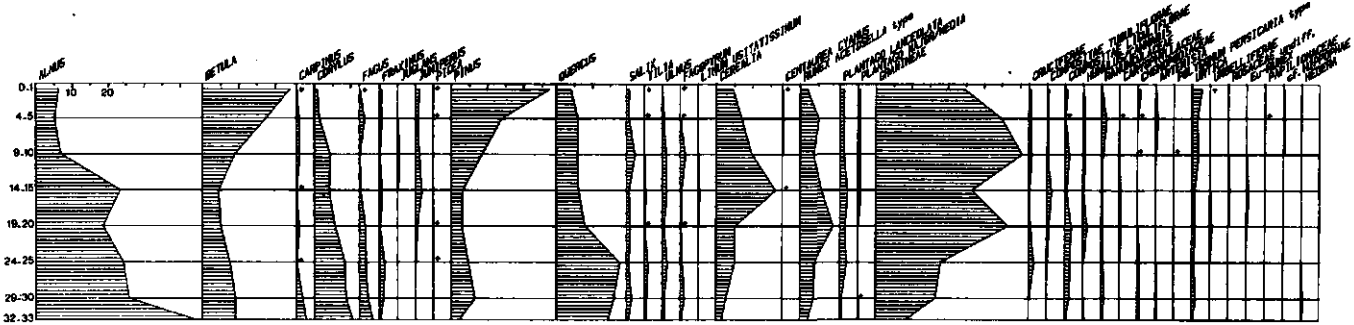


Fig. 10. Σ-pollen: trees and upland herbs (Kliplo).

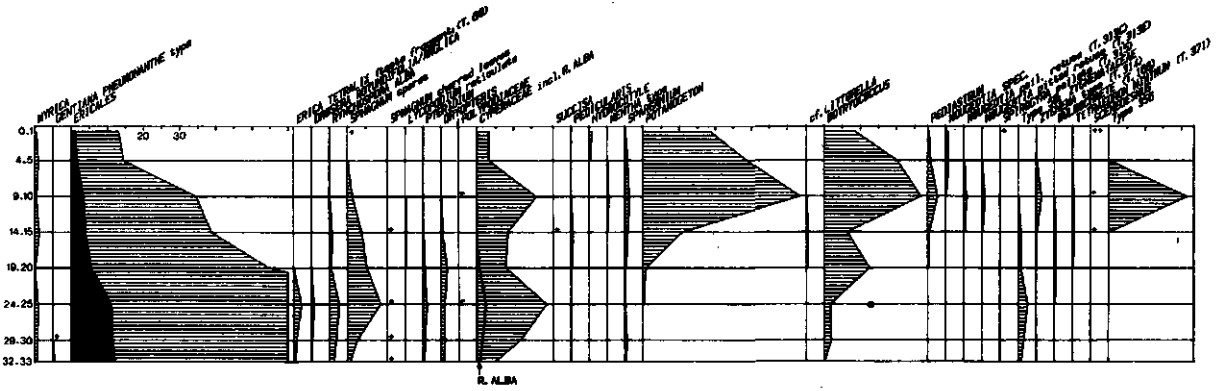


Fig. 11. Non-Σ-pollen and algae. ++ = eroded cell-walls very abundant (Kliplo).

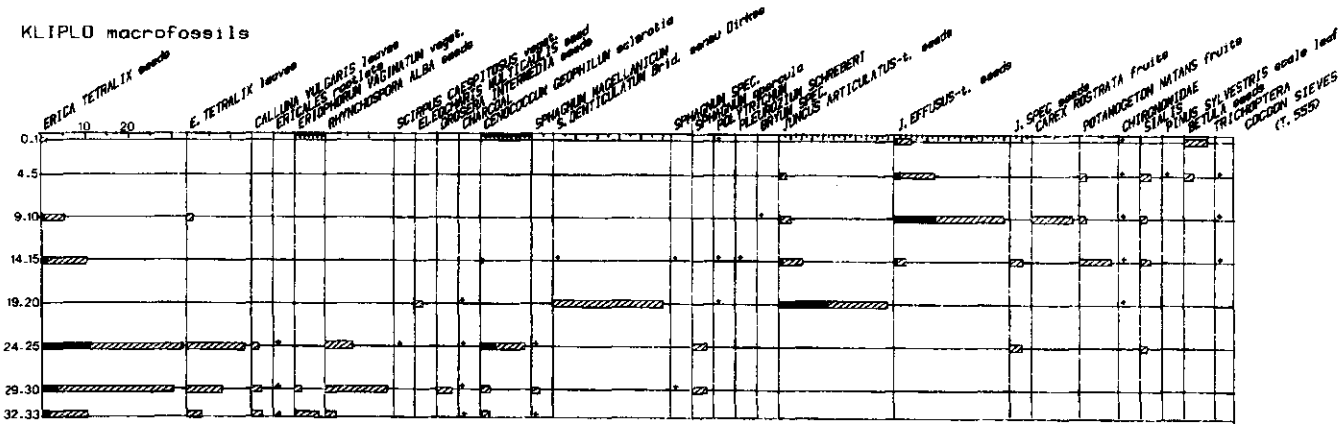


Fig. 12. Fruits, seeds and other macrofossils. Black and hatched parts of the bars represent 1/10 and 1/1 of the indicated scale respectively (Kliplo).

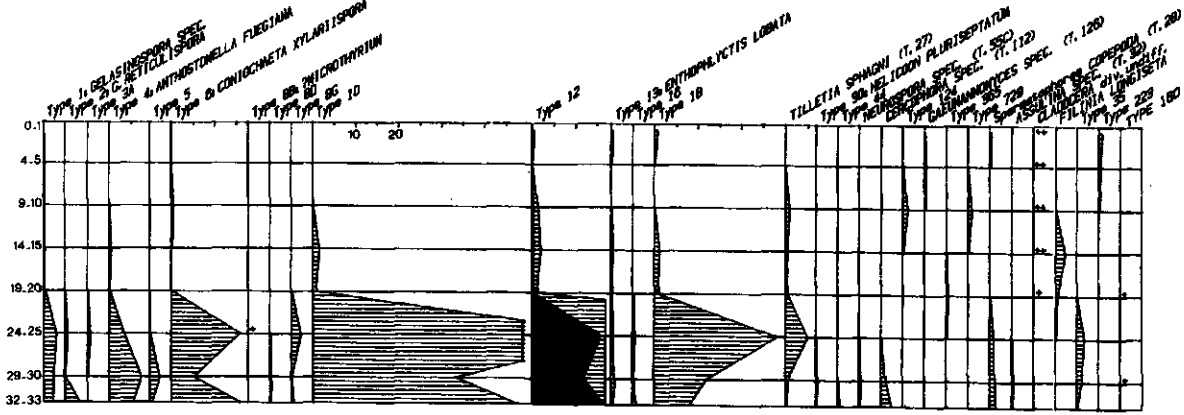


Fig. 13. Fungi, invertebrates and unknown microfossils (Kliplo).

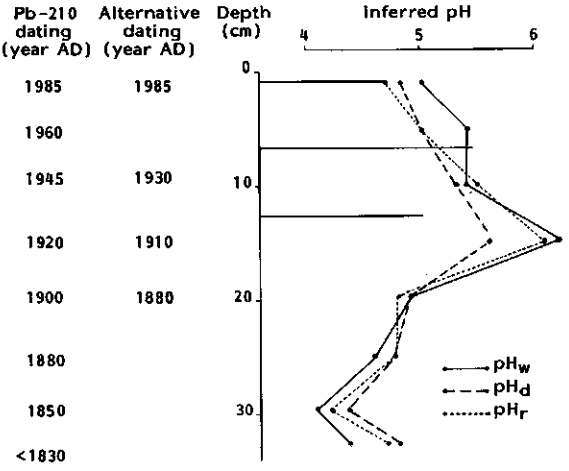


Fig. 14. Diatom-inferred pH in relation to depth. Plankton tow diatom-inferred pH indicated by horizontal bars (Kliplo).

because they were strictly local elements, as appears from the presence of Erica and Calluna leaves and Type 10 fungi, living on roots of Calluna (Figs.12 and 13) (Van Geel, 1978). The small quantities of sand in the peat indicate that disturbed sandy soils without a closed vegetation cover were present at a relatively short distance of the coring site.

The macro- and microfossils of Erica tetralix, Calluna vulgaris, Eriophorum vaginatum, Rhynchospora alba, Scirpus caespitosus, Drosera intermedia, D. anglica/rotundifolia and Sphagna are typical elements of acid, ombrotrophic bogs (Figs.10, 11 and 12). According to Van Geel (1978) most of the recorded fungi (Types 1, 2, 3a, 4, 5, 6, 10, 12 and 18) are common in, or even restricted to Sphagnum bogs (Fig.13). The relatively high percentages of the Types 10 and 12, particularly at a depth of 24-25 cm, indicate relatively dry conditions, probably during summers. The Type 58 zygmataceous spores, which were also seen by Van Geel (1978) in the initial phase of the 'Engbertsdijkveen' raised bog, indicate temporary inundations, probably during winter and spring. Pollen of Gentiana pneumonanthe and seeds of Juncus spec. are present in small quantities (Figs.11 and 12), characteristic of slightly mesotrophic conditions and a more dynamic environment than is found in raised bogs.

Both the low concentrations of diatoms and the species composition of the diatom assemblages are similar as in ombrotrophic Sphagnum bogs (e.g. Niessen, 1956; Compère, 1966; Lortie, 1983; De Vries, 1984). However, Pinnularia irrorata, which is particularly abundant in the 24-25-cm sample (Table 6) might be indicative for minerotrophic conditions (A. Mertens and H. van Dam, unpublished data). Aerophilous diatoms are well represented in this zone. At the base of the core single valves of the marine genera Cymatosira and Rhaphoneis are present. These taxa, probably imported by waterfowl or wind, were excluded from the pH calculations. The diatom-inferred pH values in this zone vary between c. 4.1 and 4.6 (Fig.14).

The relatively high percentages of Carpinus pollen indicate that the peat deposit is younger than two thousand years. Because buckwheat is grown in this area from early post-mediaeval times and is present through the whole

profile, the core would be less than 500 years old (Overbeck, 1975). However, as will be discussed later, contamination with younger sediments cannot be excluded. With Pb-210 the base of the core is dated to be deposited prior to 1840. The 24-25-cm stratum would be deposited in 1882 (±4 years) (Table 8).

Zone 2 (20-0 cm)

The two lowest samples of this zone (19-20 and 14-15 cm) contain more than 60% sand (Table 8). The sand percentage gradually decreases to 1.9 at the top of the core, as a consequence of the diminished aeolian erosion processes in the vicinity of the pool, brought about by the afforestation of the drift sands with Scots pines. The pollen percentages of pines and birches are rising from 9-10 cm level to the top of the core. The records of macrofossils of these trees in the upper two samples indicate their presence close to the coring site (Fig.12).

In the macrofossil sample from 19-20 cm leaves and stems of Sphagnum denticulatum Brid. (= S. crassicladum Warnst.) account for half of the volume of the organic material. Also many seeds of the Juncus articulatus type (including J. bulbosus) and some seeds of Eleocharis multicaulis were found (Fig.12). This assemblage is characteristic for acid, oligotrophic moorland pools. The presence of Botryococcus indicates open water too. These findings are corroborated by the interpretation of the diatom assemblage; only few aerophilous specimens were found and the diatom-inferred pH (4.9) is similar to that of the previous sample (Table 6, Fig.14).

With Pb-210 this sample is dated as AD 1903 ± 4 years (Table 8). The low pollen percentages of pines in this and the next sample, as well as the comparatively low percentage of Cerealia, would indicate a deposition well before 1900 (Fig.10).

The 14-15-cm sample was deposited in a rather different environment. Sphagnum and Juncus are present in small amounts only (Fig.12). The presence of pollen of the Sparganium emersum type, pollen and seeds of Potamogeton natans and eggs of the rotifer Filinia longiseta points to meso-eutrophic conditions (Figs.11, 12 and 13) (Radwan, 1976; Mäemets, 1983). The diatoms Achnanthes minutissima, Fragilaria virescens, and Gomphonema gracile (Table 6) are known from moderately eutrophied moorland pools (Van Dam and Kooyman-van Blokland, 1978). The diatom-inferred pH is c. 6 (Fig.14).

According to the Pb-210 data this sample would be deposited between 1918 and 1923 (Table 8). The peak of Cerealia pollen (Fig.10) is associated with the intensification of agriculture by reclamation of moorlands around the turn of the 19th century (Booij and Van Oosten, 1978; Bakker et al., 1986).

In the upper three samples of the profile Pediastrum and Scenedesmus indicate meso- or eutrophic conditions, just like Potamogeton natans (Fig.11). Seeds of the Juncus articulatus type decline at the favour of J. effusus type seeds. The latter taxon is associated with disturbance (most often by eutrophication) of originally oligotrophic shallow pools. The decrease of Achnanthes minutissima, Fragilaria virescens, and Gomphonema gracile might indicate less eutrophic conditions than in the 14-15-cm sample. Brachysira vitrea and Cymbella rabenhorstii, characteristic of oligo-mesotrophic conditions (Jørgensen, 1948; Niessen, 1956), have their maximum in the 9-10-cm sample and are decreasing to the top of the core. The diatom diversity is maximal (high number of taxa and low dominance) in this mesotrophic stage (Table 6). The diatom-inferred pH decreases from c. 5.4 at 9-10 to c. 5.0 at the top of the core (Fig.14).

According to the Pb-210 data the 9-10-cm sample would be deposited

TABLE 9

Comparison of dating methods

Pool	Depth (cm)	Pb-210 dating	Alternative dating	Alternative method
G	0-3	1966-1985	1964-1985	diatoms, cladocerans
G	3-4	1961-1967	1950-1960	diatoms
G	6-8	1900-1949	1915-1920	pollen, diatoms
G	10-11	ca 1830	ca 1900	diatoms
G	11-13	<1840	ca 1870	pollen
G	19-30	<1840	<1850	pollen, diatoms, maps
G	34-39	<1840	<1840	pollen, diatoms, maps
K	9-10	1942-1948	ca 1930	pollen
K	14-15	1918-1923	ca 1910	pollen
K	19-20	1900-1907	ca 1880	pollen

G = Gerritsfles, K = Kliplo.

between 1942 and 1948 (Table 8). The rise of the percentage of pollen of pines and birches follows the massive planting from 1906 onwards.

The sedimentation rate of the predominantly organic sediments between 1935 and 1985 was c. 2 mm per year. If the predominantly sandy sediments between 19-20 and 9-10 cm depth would be deposited between 1870 and 1935 the sedimentation rate would be about 1.5 mm per year.

5 DISCUSSION

5.1 Gerritsfles

Dating both by Pb-210 and alternative methods of the upper 7 cm of the core shows consistent results (Table 9). With Pb-210 the deeper layers are dated a few decades older than with alternative methods, probably due to an anomalous high Pb-210 content at th 6-7 cm level in the activity-depth profile (Van der Wijk and Mook, in press). Therefore, we prefer to use the ages obtained from alternative methods at depths greater than 7 cm.

Hesselink (1915) and Lorié (1916) assume that the gully, depicted as a marsh in 1826, existed earlier as a dry depression in the heathlands. Stagnation of water became possible after blocking up the western end of the gully by a dam of aeolian drift sand. Although aeolian drift sand is very permeable to vertical percolation of water, it can be rather impermeable to lateral flow. Other moorland pools in The Netherlands have been formed in this way too (e.g. Zonneveld, 1965; Van Zuidam, 1980).

Vertical drainage was impeded by the presence of a more or less impermeable illuvial horizon of amorphous humus and sesquioxides. Such horizons are often present in heathland areas, and small marshes or intermittent pools may develop at such localities. A placic horizon (iron pan) can be formed within a century where waterlogged soil, poor in oxygen, overlies a well drained soil, rich in oxygen (Crompton, 1952, 1956; Proudfoot, 1958; Buurman, 1984). The formation of a permanent water body on such an horizon is apparently favoured if it is covered with either a layer of drift sand or with an unusually thick layer ($\geq$0.8 m) of eluviated sand. During overflow of the pool at high water levels a vertical wall of iron concretions is built up at the brim, by leaching of iron from the ferrugineous cutans of the grains of drift sand blown into the pool, and subsequent precipitation by oxidation (Voorwijk and Hardjoprakoso, 1945; Schimmel and Ter Hoeve, 1952; Stoutjesdijk, 1959; Zonneveld, 1965; Jungerius

and Marsman, 1971). This process can take place very rapidly; in the 'Deelensche Heide', about 8 km south of Gerritsfles, permanent moorland pools developed from a dry heath within fifty years. The annual increase of the mean water level in these pools was between 0.5 and 1 cm (S. van der Werf, personal communication, 1986).

During the first half of the 19th century the Gerritsfles site rapidly evolved towards a pool, presumably because the growth of the vertical wall of concretionary iron was stimulated by sand, blown in from the 'Harskamperzand' (Zone 1 of the profile). The weak pollution was probably due to sheep excrements.

The water level gradually increased and Gerritsfles became a shallow, acid, oligotrophic pool (Zone 2). In this stage the water was too deep for sheep to cross the pool regularly, so pollution with excrements stopped. As the pool did not desiccate each summer any longer, the rate of decomposition of organic material decreased and humic substances accumulated.

When the water level further increased the pool became sufficiently deep for the washing of sheep around 1850. The sheep introduced a considerable amount of nutrients into the pool each year and allowed meso- and eutraphent species to grow. Such changes were also seen in the diatom assemblages of the pool 'Deelensche Wasch', 8 km from Gerritsfles (Leentvaar, 1984). Both the annual variations in precipitation excess and casual drainage of the pool in order to catch fish caused fluctuations of the water level (Zone 3). The eutrophication caused an increase of pH, as was observed in soft-water lakes that were fertilized experimentally with phosphate and/or nitrate (Schindler et al., 1985) and in moorland pools that were eutrophicated by agricultural drainage water, fishing or bathing (Van Dam and Kooyman-van Blokland, 1978). Probably Gerritsfles was stocked with fish after eutrophication, as fish cannot live in acid, oligotrophic waters (Haines and Johnson, 1982).

Due to the decline of sheep farming and the planting of pines the drift sand stabilized at the turn of the 20th century. As less sand was blown into the pool the sediments became more organic. The growth of the vertical wall of iron concretions ended and both the surface area and the depth did not increase any longer (Zone 4a). The reduced input of nutrients by sheep and depletion of nutrients by annual overflow of the pool led to a process of oligotrophication, with a concomitant decrease of pH and fish. The rate of the decrease of the nutrient level and pH may have been slowed down by the input of nutrients by swimmers from c. 1920 through c. 1960. Particularly after 1950 the increased acidity of dry and wet atmospheric deposition contributed to a further decrease of the pH, as described by Van Dam (in review) (Zone 4b).

5.2 Kliplo

Pb-210 inferred dates are systematically 10 to 20 years younger than the dates inferred from changes in Pinus and Cerealia pollen in three samples from the top of the core. The various mechanisms, e.g molecular redistribution of Pb-210 due to bacterial activity or diffusion, that may explain such differences, are beyond the scope of this paper. The uncertainty in the absolute ages of these samples will not affect the validity of the conclusions.

Soon after its formation Kliplo developed into a bog, which was slightly mesotrophic, probably due to inflow of water from the surrounding area (Zone 1). The high proportion of aerophilous diatoms in the 24-25-cm layer indicates relatively dry conditions and might be associated with artificial

drainage of the bog, prior to excavation.

Apparently the Kliplo bog was excavated for the larger part around 1850 and an aquatic community, characteristic for humic-acid, oligotrophic pools (19-20 cm), on top of a hiatus, started to develop. The excavation might have disturbed the original stratification at the base of the core.

Around 1900 a meso-eutrophic system (pH c. 6) had developed. The exact causes of nutrient enrichment are not documented by the historical information at our disposal, and only speculations are possible. Staring (1861) mentions the great activity of the drift sand area around Kliplo, which caused a continuous flux of sand into the pool. As the thermal conductivity of water saturated quartz sand is 5-10 times higher than that of peat (De Vries, 1963) the temperature of the sediment increased more rapidly in spring, the heat penetrated deeper into the sediment and higher summer temperatures were reached in the sediment. As a consequence the decomposition of the organic sediment would have been accelerated, and the nutrient levels in the overlying water might have been increased to the meso-oligotrophic level that is required for a good development of Sparganium angustifolium. This species has its optimum in moorland pools with a sandy-peaty bottom in or near aeolian drift sands and is often accompanied by nitrophilous plant species (Van Ooststroom and Reichelt, 1964). A further increase of the nutrient level might be due to sheep washing, as a sandy eastern shore, rare in other pools in the area, makes Kliplo suitable for this purpose. Moreover, Kliplo might have been used as a duck-decoy, like the nearby pool Schurenberg (G.J. Baaijens, personal communication, 1986). The abandoned ditch in the northeastern corner of the pool might be a remnant of a pipe of the decoy. The belt of reed (Phragmites australis), certainly not autochthonous, might be derived from a reed-mat that was used as a shelter for the decoy-man and his dog.

After dissolution of the sheep flock, finishing decoying, and fixation of the drift sand at the turn of the 20th century, a process of oligotrophication started, which is seen as a decrease of meso- and eutraphent organisms and the diatom-inferred pH in the most recent sediments. The increased acidity of atmospheric deposition is an additional cause for this process. As assessed from changes in the assemblages of desmids and macrophytes since c. 1920, eutrophication of this pool has been reported by Coesel and Smit (1977) and Van Dam (in review). The discrepancy is difficult to explain.

6 GENERAL DISCUSSION AND CONCLUSIONS

Diatom-inferred pH values in undisturbed soft-water lakes in Northern Europe and Northern America have been constant or departed from initial values between 5 and 7 with a decrease of less than 0.1 unit per millennium between 8000 and 100 yr BP. The slow and long-term acidification is a natural process in interglacial periods. More recently the rate of acidification of these lakes has increased to over 0.1 unit per decade, due to acid atmospheric deposition (Andersen, 1966, 1967; Renberg and Hellberg, 1982; Jones et al., 1986; Whitehead et al., 1986).

Our results indicate that the moorland pools studied, including Achterste Goorven (Dickman et al., in press), are younger and much more dynamic systems than the lakes mentioned. Secular changes in our pools exceed millenary changes in these lakes.

After the origin of Achterste Goorven in the early Holocene and of Kliplo in the early Subatlantic both pools developed into oligotrophic bogs. Following excavation of the bogs in the 19th century, the pH-values of the

pools increased from 4-5 to c. 6 around 1900, due to eutrophication by external sources, and later on decreased to present values between 4 and 5, when eutrophication stopped and acid atmospheric deposition increased.

Gerritsfles is even more dynamic. This pool formed spontaneously in a depression in a humid heath, less than two centuries ago, by pedological processes that are associated with the presence of aeolian drift sands. As these sands were formed from the semi-natural heathlands by overgrazing with sheep, the Gerritsfles pool can be considered as an artefact. The chemistry was influenced by anthropogenic processes too. The initial pH-value between 4 and 5 increased to c. 6 around 1900, due to eutrophication by washing of sheep, and later decreased, like in Achterste Goorven and Kliplo.

Beyens (1984) studied the diatoms in the sediments of a Belgian moorland pool, which were deposited since 7000 yr BP. Indicators for strong organic acidity (pH < 4.5) were found in the lower part of the core. Throughout the core the diatoms indicated strongly acid conditions. The impact of increased acid atmospheric deposition is reflected by the increase of Eunotia exigua, an indicator of mineral acidity, since 1850.

Thus weakly acid conditions (pH 5-6) at our study sites were artificial and ephemeral. For the present it seems impossible to separate the contributions of acid atmospheric deposition and the discontinuation of eutrophication to the acidification of these pools. Consequently it is hard to determine when acidification by acid atmospheric deposition started.

Presumably many isolated, now ostensibly pristine, moorland pools have been anthropogenically eutrophied in the past. Therefore Leuven et al. (1986) probably overestimated the extent of acidification by acid atmospheric deposition on moorland pools in The Netherlands, as assessed from comparison of old and recent chemical and biological records, without paying much attention to changes of management of the study sites.

At least in the intensively cultivated region of Western Europe documented evidence on human influence upon study sites and their surrounding landscapes is a prerequisite to obtain proper conclusions about the history of surface water acidification.

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HOOFDSTUK 7

ALGEMENE DISCUSSIE

1 Verloop van het onderzoek

Mede doordat de auteur het onderhavige onderzoek naast andere werkzaamheden uitvoerde, duurde het meer dan tien jaar voordat het voltooid was. Aan deze lange periode zijn verschillende voordelen verbonden. Zo was er gelegenheid zelf materiaal voor het opstellen van tijdreeksen te verzamelen en te bewerken, hetgeen de homogeniteit van de waarnemingen ten goede is gekomen. De verzuring en alkalinisering van vennen kon op verschillende tijdschalen worden bestudeerd. Het accent van het onderzoek verschoof daarbij van een diagnostische beschrijving naar het volgen en interpreteren van processen die zich bij de verzuring van vennen voordoen.

Een nadeel van de lange duur van het onderzoek was dat de nomenclatuur en taxonomie van kiezelwieren, die als voornaamste biologische indicatoren voor de zuurgraad zijn gebruikt, in de onderzoekperiode aan sterke veranderingen onderhevig waren. Daardoor zijn die namen uit de verschillende hoofdstukken niet altijd direct vergelijkbaar. Latere onderzoekers kunnen de determinaties controleren en aanpassen aan nieuwe inzichten door studie van de monsters en preparaten, opgenomen in de collectie van het Rijksinstituut voor Natuurbeheer (Leersum). Bij het Hugo de Vries-laboratorium van de Universiteit van Amsterdam zijn duplicaten van de preparaten gedeponeerd.

2 Collecties en archieven

Bij dit onderzoek is veel gebruik gemaakt van een deel van de algenmonsters, die in de eerste helft van deze eeuw door J. Heimans in enkele honderden vennen in het hele land werden genomen en sindsdien zorgvuldig worden geconserveerd in het Hugo de Vries-laboratorium (Schroevers 1980). Ook uit andere verzamelingen werd materiaal betrokken.

Beijerinck (1926) vermeldt dat hij zijn monsters uit ongeveer 200 Drentse vennen zorgvuldig had geconserveerd ten behoeve van toekomstige onderzoekers. Het materiaal is in de jaren zestig, samen met aanvullende documentatie, verdwenen na een schoonmaakbeurt van het biologisch station te Wijster, dat door Beijerinck werd opgericht. Omdat hij van de meeste door hem onderzochte locaties de exacte soortensamenstelling niet opgeeft, is deze nu ook niet meer na te gaan. Blijkens zijn tekeningen voldoen sommige van zijn determinaties niet aan de hedendaagse eisen. Aanpassing is helaas niet meer mogelijk.

Van Dam & Beljaars (1984) en Arzet & Van Dam (1986) bestudeerden kiezelwieren op herbariummateriaal van hogere planten en mossen, dat vanaf 1839 in Duitse laag-alkaliene wateren werd verzameld. Door vergelijking met recent verzameld materiaal kon verzuring van een aantal van deze wateren worden vastgesteld.

Deze voorbeelden tonen aan dat het voor toekomstige milieu-onderzoekers van groot belang is dat de huidige botanische verzamelingen op adequate wijze worden beheerd en onderhouden.

Bij het zoeken naar oude gegevens over de onderzochte locaties constateerde ik herhaaldelijk onvolledige verslaglegging van verzamelde gegevens en onvoldoende ontsluiting daarvan met al of niet geautomatiseerde documentatiesystemen. Zo konden b.v. nog geen twintig jaar oude chemische gegevens, waarvan bekend was dat ze verzameld waren, ondanks uitgebreide speurtochten

langs archieven en privé-personen, niet meer worden achterhaald. In de archieven van het Rijksinstituut voor Natuurbeheer, het Staatsbosbeheer, de Hydrobiologische Vereniging en de Vereniging tot Behoud van Natuurmonumenten in Nederland werd veel waardevol materiaal aangetroffen. Vaak werden voor dit onderzoek belangrijke gegevens slechts bij toeval als terloopse opmerking gevonden in stukken over geheel andere onderwerpen. Nog sterker was dit het geval bij gegevens over het beheer van enkele vennen in vorige eeuwen, die slechts met hulp van historici in gemeentelijke, provinciale en rijksarchieven konden worden opgespoord.

Ten gevolge van onvolledige verslaglegging kunnen latere onderzoekers fouten maken. Zoals reeds vermeld in Hoofdstuk 1 werd de pH van vennen tijdens het z.g. S.O.L.-onderzoek met indicatorpapier gemeten, waardoor de waarnemingen onbruikbaar zijn. De methode is destijds niet in de excursieverslagen vermeld, waardoor de waarnemingen later door verschillende onderzoekers ten onrechte zijn gebruikt om pH-dalingen in een aantal vennen te illustreren.

Het verdient derhalve aanbeveling om ongepubliceerde gegevens, voorzien van een goede beschrijving van de gebruikte bemonsteringstechnieken en analysemethoden, in meer dan één archief te deponeren en de gegevens met documentatiesystemen te ontsluiten.

3 Zuurgraadverschillen in ruimte en tijd

De pH is een belangrijke conditionele milieufactor voor de samenstelling van venlevensgemeenschappen. In de volgende discussie wordt de pH, zoals die direct is gemeten of is geschat op grond van de voorkomende organismen, gebruikt om de onderzochte vennen, met hun levensgemeenschappen, op eenvoudige wijze te karakteriseren, hoewel andere factoren de samenstelling van de levensgemeenschap mede bepalen. In de Nederlandse vennen is de mate van voedselrijkdom sterk gecorreleerd met de pH (Hoofdstuk 2). In het extreme milieu van sterk zure vennen is het soortenassortiment zeer beperkt, hoewel er duidelijke verschillen zijn tussen vennen waar de lage pH veroorzaakt wordt door organische zuren (zoals vroeger meestal het geval was) en vennen waar deze veroorzaakt wordt door minerale zuren (zoals nu vaak het geval is). In wateren met hogere pH-waarden kunnen meer soorten leven en kan de soortensamenstelling tussen wateren met een zelfde pH sterker verschillen dan in wateren met een lage pH.

Uit Hoofdstuk 2 blijkt dat de pH in geïsoleerde vennen tussen ca 1920 en 1975 is gedaald. De daling werd toegeschreven aan de invloed van zure neerslag. In vennen die werden belast met voedingsstoffen, afkomstig van landbouw, visserij, of recreatie, was de pH-daling minder sterk dan in geïsoleerde vennen of was de pH zelfs toegenomen.

In Hoofdstuk 3 werden 16 geïsoleerde vennen bestudeerd. Uit oriënterend literatuuronderzoek was niet gebleken dat ze in deze eeuw door toevoer van voedingsstoffen uit de omgeving waren belast. Rond 1920 liep de pH tussen de vennen uiteen van ca 4 tot ca 6, in 1978 waren de verschillen afgenomen en lag de pH tussen 3,7 en 4,6. De pH was het minst gedaald in vennen met humeus water en een venige bodem, waar de sulfaatreductie zeer intensief is, en het meest in vennen met helder water en een zandige bodem.

Het onderzoek in de volgende hoofdstukken concentreerde zich op drie vennen, Achterste (A.) Goorven, Gerritsfles en Kliplo, waarvan naast oude algenmonsters relatief veel oude gegevens over chemie, biologie en beheer beschikbaar waren. Elk van deze vennen vertegenwoordigt een uiterste van de biologische en chemische variatie die in Hoofdstuk 2 werd behandeld. Met elkaar zijn ze representatief voor de 16 vennen van Hoofdstuk 2. De

chemische samenstelling van A. Goorven en Gerritsfles komt goed overeen met die van ruim honderd zure laag-alkaliene wateren, die door Kersten (1985) werden bestudeerd. Voor Kliplo is dit in mindere mate het geval.

Uit Hoofdstuk 4 blijkt dat de mate van verzuring afhankelijk is van de vorm van het waterbekken. Een deel van de zwavel- en stikstofverbindingen, die door atmosferische depositie in het ven terechtkomen, wordt in gereduceerde vorm in de onderwaterbodem vastgelegd. De reductieprocessen hebben een bufferende werking op de verzuring. In recente extreem droge zomers (b.v. 1959, 1976) viel een deel van de venbodem droog en werden deze verbindingen geoxydeerd, waarbij zuren werden gevormd. In vroegere droge zomers (b.v. 1921) was dit laatste niet het geval. In komvormige vennen valt een kleinere fractie van de bodem droog dan in schotelvormige vennen en is de verzuring ook geringer. De duur van herstel na een droge zomer hangt af van de verblijftijd van het water (3-6 jaar) en varieert van vijf tot tien jaar. De stijging van de pH in de herstelperiode is het gevolg van alkaliniteitsproduktie door sulfaatreduktie en denitrificatie. Deze processen worden bevorderd door de beschikbaarheid van organische stof, die zich eerder had opgehoopt, doordat de afbraakprocessen ten gevolge van verzuring werden geremd. In de eerste jaren na de droogte van 1976 was het calciumgehalte van deze drie en andere vennen (Kersten 1985) hoger dan in de periode ervoor of gedurende de laatste paar jaar. Het model van Henriksen (1980), waarmee de vroegere alkaliniteit berekend wordt op grond van de huidige calciumconcentratie, kan daarom niet gebruikt worden om de mate van verzuring van Nederlandse vennen te berekenen. De door Schuurkes & Leuven (1986) op dit model gebaseerde schatting van het percentage verzuurde laag-alkaliene Nederlandse wateren is daarom te hoog.

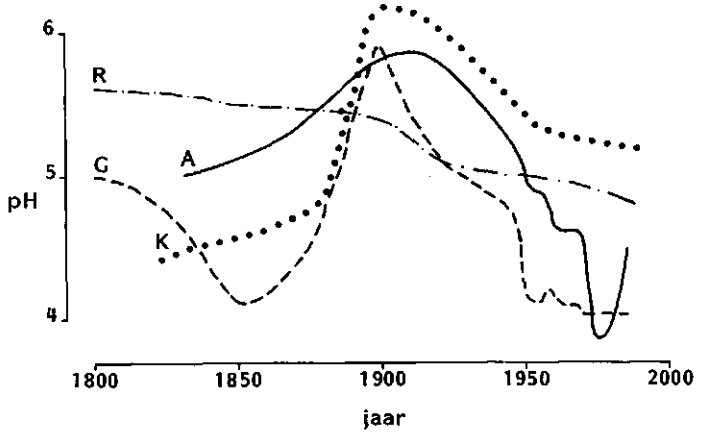

Fig. 1. Veranderingen in de pH van Achterste Goorven (A), Gerritsfles (G), Kliplo (K) en Round Loch of Glenhead, Schotland (R).

In de Hoofdstukken 5 en 6 werd de pH-ontwikkeling vanaf ca 1800 gereconstrueerd. De resultaten zijn, samen met die uit Hoofdstuk 4 en metingen in 1985 en 1986, enigszins geschematiseerd in Figuur 1 weergegeven. Ter vergelijking is het pH-verloop in een kalkarm Schots meer opgenomen, dat min of meer representatief is voor verzurende Europese meren (Flower & Battarbee

1983). De oorspronkelijk lage pH-waarden in de vennen bereikten een maximum rond 1900, door toevoer van landbouwwater (A. Goorven) of door het wassen van schapen (Gerritsfles). Kliplo werd waarschijnlijk als schapenwas en/of als eendenkooi gebruikt. Na het staken van de toevoer van voedingsstoffen daalde de pH weer, hetgeen mede is bevorderd door de toename van zure atmosferische depositie.

De pH-veranderingen in de onderzochte vennen zijn aanzienlijk ingewikkelder dan die in verzurende meren, waar de pH in de laatste millennia vrijwel constant was en pas in de laatste eeuwen of decennia een sterke, monotone, daling vertoont (Battarbee & Charles 1986). Door het kleine watervolume en het relatief grote oppervlak zijn vennen gevoeliger voor externe beïnvloeding dan meren.

4 Veranderende vennen in een veranderend landschap

Vennen zijn karakteristiek voor het flauw naar zee afhellende zandlandschap van de Noordwesteuropese laagvlakte, dat uniek is op het noordelijk halfrond (De Smidt 1984). In de vorige eeuw lagen in ons land duizenden vennen te midden van uitgestrekte heiden en zandverstuivingen, waar het zicht vaak tot de horizon reikte. Dit landschap was het produkt van begrazing en overbegrazing door schapen, die voornamelijk werden gehouden om te voorzien in de mestbehoefte van de bouwlanden.

Veel vennen zijn ontstaan op lage plaatsen in heidevelden, daar waar zich een waterdicht ijzeroerlaagje gevormd heeft. Zonneveld (1965) beschouwt dit als een extreem geval van humuspodzolvorming, zoals die alleen onder een heidevegetatie mogelijk is. Uit de ontstaansgeschiedenis van de Gerritsfles, beschreven in Hoofdstuk 6, en de aldaar geciteerde literatuur, blijkt dat het ontstaan van dergelijke vennen bevorderd werd door actief stuifzand en nog plaatsvond tot in de vorige eeuw.

Veel vennen hadden een functie in het oude landbouwsysteem en dienden onder meer voor het steken van turf (waardoor het open water van veel vennen ontstond), het wassen van schapen, roten van vlas en kweken van vis. Het water werd o.a. gebruikt voor het brouwen van bier. Namen als Klotven, Wasmeer, Vlasven, Pastoorsweijer en Brouwkuip herinneren hier nog aan. Afhankelijk van de mate van menselijke beïnvloeding ontwikkelden zich verschillende levensgemeenschappen in de vennen. Dit wordt o.a. geïllustreerd door de ontwikkelingen in A. Goorven, Gerritsfles en Kliplo (Hoofdstukken 5 en 6). In de eerste twee vennen kwamen planten uit het oeverkruidverbond (waterlobelia en oeverkruid) in het begin van de 19e eeuw niet of nauwelijks voor. Pas nadat de pH door externe toevoer van voedingsstoffen in de tweede helft van de 19e eeuw tot waarden tussen 5 en 6 was gestegen, konden deze planten zich ontwikkelen. In Kliplo verscheen na eutrofiëring de drijvende egelskop, die ecologisch verwant is aan soorten uit het oeverkruidverbond (Westhoff & Den Held, 1969). Behalve enige voedselverrijking stimuleerde een beheer van 'bodemverjonging', d.w.z. een regelmatige verwijdering van het organische sediment, het voorkomen van zeldzame planten en dieren (Westhoff & Van Leeuwen 1959, Westhoff 1979, Schroevers 1979, Arts 1986). In sommige gebieden werden vennen door sloten met elkaar en met beeklopen verbonden en werd relatief voedselrijk water aangevoerd. In de geleidelijke overgangen van voedselarm naar voedselrijk was een grote verscheidenheid aan levensvormen (b.v. Hoofdstuk 2). De menselijke activiteiten veroorzaakten een toename van de biologische verscheidenheid.

Na de uitvinding en toepassing van kunstmest verloren de heiden hun betekenis als mestbron voor de landbouw en grote oppervlakten ervan werden ontgonnen en bebost. De meeste stuifzanden werden door bebossing vastgelegd.

Vennen in de ontginningen die niet verdwenen door ontwatering of egalisatie verloren hun voedselarme tot matig voedselrijke karakter door overmatige bemesting. Bijzondere soorten hogere planten ontbreken in dergelijke vennen, maar wel zijn soms bijzondere soorten kiezelwieren aanwezig (Hoofdstuk 2).

Door bebossing van heiden en stuifzanden en het dichtgroeien van onbeboste delen hiervan met opslag van berken en dennen, is de vereiste mate van dynamiek in deze landschapstypen, voornamelijk veroorzaakt door de wind, verloren gegaan. Zowel het ontstaan van nieuwe vennen als de instandhouding van gemeenschappen uit het oeverkruidverbond, die voorkomen op een door windwerking of anderszins kaal gehouden zandbodem, zijn daardoor vrijwel onmogelijk geworden (Hoofdstuk 6).

De natuurbescherming deed veel moeite om de vennen in de overgebleven heiderestanten en heide- en stuifzandbebossingen te vrijwaren van overmatige verrijking met voedingsstoffen. Sloten die landbouwwater aanvoerden moesten daartoe worden afgedamd, maar daardoor veranderden de eertijds geleidelijke overgangen van voedselrijk naar voedselarm in sprongsgewijze overgangen. Vestiging van kokmeeuwenkolonies en overmatig gebruik van vennen als zwemwater moesten worden tegengegaan. Door het verdwijnen van de oude gebruiksvormen van de vennen verdwenen de kleine verschillen in voedselrijkdom grotendeels en de levensgemeenschappen van geïsoleerde vennen convergeerden, mede door de invloed van zure neerslag, steeds meer naar een zelfde type van wateren met hoge gehalten aan minerale zuren. Hierin zijn knolrus en veenmos de meest voorkomende macrofyten en Eunotia exigua is het dominante kiezelwier.

De tweedeling in overmatig bemeste, alkalische vennen en verzuurde vennen wordt geïllustreerd door Figuur 5 van Hoofdstuk 2. Vennen met pH-waarden tussen 5 en 6, waar o.a. soorten uit het oeverkruidverbond en zeldzame sieralgen thuishoren (Coesel e.a. 1978), ontbreken nagenoeg. Uit de gegevens van Arts (1986), Arts e.a. (1986) en Schuurkes & Leuven (1986) blijkt dat een dergelijke ontwikkeling zich ook landelijk heeft voorgedaan. Het aantal vindplaatsen van drie belangrijke soorten uit het oeverkruidverbond (biesvaren, waterlobelia en oeverkruid) is na 1980 meer dan 90% lager dan voor 1960. Van de sieralgen leidt nog slechts ca 10% van het aantal inheemse soorten een onbedreigd bestaan (Coesel 1986). Terecht stelt Westhoff (1979) dat het behoud van levensgemeenschappen van halfnatuurlijke landschapselementen zoals matig voedselarme vennen een der moeilijkste problemen van de Europese natuurbescherming is.

5 Criteria en normen

Ten behoeve van de bestrijding van waterverzuring zijn normen voor zure atmosferische depositie noodzakelijk. Daartoe is het nodig om eerst vast te stellen wat de gewenste toestand van de levensgemeenschappen van vennen is. Vervolgens moet worden vastgesteld bij welk niveau van zure atmosferische depositie deze, of een andere wenselijk geachte, toestand kan voortbestaan of kan worden ontwikkeld.

5.1 Vennen

Diemont (1984) en Bieleman (1985) toonden aan dat het heidelandbouwsysteem sinds de 17e eeuw veel sterker is veranderd dan eerder werd verondersteld, zoals nu ook bij vennen het geval blijkt te zijn. Diemont schrijft: "Of de heide paars moet zijn, paars/groen of groen, kan niet uit het verleden gedestilleerd worden, daarvoor heeft de heide te veel verschillende gezichten gehad. Wij zullen zelf moeten uitmaken hoe de heide er moet uitzien."

Dit is, mutatis mutandis, ook het geval voor vennen. Om te beoordelen welke ontwikkelingen gewenst, dan wel ongewenst zijn, is er behoefte aan criteria voor beoordeling. Daar het behoud en het bevorderen van verscheidenheid het kernthema van het natuurbeheer is (b.v. Westhoff 1984) is deze verscheidenheid een belangrijk criterium. De verscheidenheid omvat zowel de diversiteit aan soorten op een bepaalde plaats (diversity in Hoofdstuk 3) als de mate waarin de soortensamenstelling op een plaats afwijkt van die op andere plaatsen (dissimilarity in Hoofdstuk 3). Vooral vroeger was er een grote verscheidenheid aan soorten organismen binnen en tussen vennen, die werd bevorderd door verschillen in menselijke beïnvloeding tussen vennen. Voedselarme tot matig voedselrijke vennen leveren een belangrijke bijdrage tot de verscheidenheid van oppervlaktewateren in nationaal en internationaal verband, daar de levensgemeenschappen van deze vennen sterk afwijken van die van voedelrijke oppervlaktewateren, die in de meerderheid zijn. Schroevers (1975) vestigt ook de aandacht op onvervangbaarheid als maatstaf bij de beoordeling van natuurwaarden. Voedselarme systemen zijn moeilijker te creëren - en daardoor moeilijker te vervangen - dan voedselrijke systemen.

Bij het beoordelen van de kwaliteit van een water in het algemeen, en van een ven in het bijzonder, wordt met behulp van bovengenoemde criteria getoetst in hoeverre een bepaald water zijn functie als natuurgebied vervult. In de praktijk wordt de aangetroffen toestand daartoe vaak vergeleken met een standaardtoestand of referentie (Schroevers 1984). Een uniforme standaardtoestand is voor vennen, gezien het belang van de verscheidenheid, niet gemakkelijk te definiëren. Schuurkes & Leuven (1986) rapporteren over een omvangrijk onderzoek naar oorzaken, omvang en effecten van waterverzuring in Nederland. Zij definiëren hun standaardtoestand niet expliciet, maar als zij stellen: "Zwak gebufferde, voedselarme wateren worden van oorsprong gedomineerd door een variatie van soorten uit het oeverkruidverbond, zoals oeverkruid (Littorella uniflora), waterlobelia (Lobelia dortmanna) en biesvaren (Isoetes lacustris)", mag worden aangenomen dat dit hun standaardtoestand is. Uit de Hoofdstukken 5 en 6 blijkt dat standplaatsen voor soorten uit het oeverkruidverbond tot in de vorige eeuw relatief gemakkelijk te creëren waren, uitgaande van voedselarme beginsituaties. Thans is dit, mede door atmosferische depositie, niet meer het geval en zijn systemen met soorten uit het oeverkruidverbond minder gemakkelijk vervangbaar dan een eeuw geleden. Vennen met soorten uit het oeverkruidverbond leveren een belangrijke bijdrage aan de verscheidenheid, maar dat kan met sommige andere vennen ook het geval zijn. Een meer algemene omschrijving van de standaardtoestand gaat uit van de onwenselijkheid van nivellering door sterke voedselverrijking en/of verzuring en laat daarbinnen ruimte voor het optreden van een groot aantal verschillen.

De standaardtoestand is dan een ven met een pH lager dan ca 6,5, waarin soorten uit voedselrijke omgeving niet of weinig voorkomen en de verzuringsindicator Eunotia exigua niet of in slechts geringe hoeveelheden (relatieve hoeveelheid < 20%) voorkomt. Dit gaat, althans in de wat grotere en diepere vennen, vaak samen met slechts geringe hoeveelheden veenmos en knolrus. Deze toestand is een omschrijving van de waterkwaliteitsdoelstelling van het hoogste niveau, maar komt niet altijd overeen met de natuurlijke toestand, die in het Indicatief Meerjarenprogramma Water 1985-1989 (Rijkswaterstaat 1986) als streefdoel wordt gezien. Het nalaten van oogsten of ander menselijk gebruik, dat in het IMP als bestaansvoorwaarde voor dit niveau wordt genoemd, is daarom niet altijd wenselijk.

5.2 Depositie

Schuurkes & Leuven (1986) presenteren normen voor depositieniveaus van (potentieel) verzurende stoffen, die zijn gebaseerd op laboratoriumexperimenten met mini-ecosystemen ('kunstvennen') en bodem-waterkolommen met een inhoud van enkele liters, waaraan kunstmatig regenwater werd toegevoegd. Zowel in de kunstvennen als in de kolommen treden na verloop van tijd zeer hoge sulfaatconcentraties op en verloopt het bufferende sulfaatreductieproces kennelijk in mindere mate dan in echte vennen (Hoofdstukken 3 en 4). In de kolommen is ook het - eveneens bufferende - denitrificatieproces sterk geremd. De experimenten duurden relatief kort (kunstvennen 2 jaar, kolommen 12 weken) en er is geen aandacht geschonken aan het droogvallen van de venbodem, hetgeen op langere termijn van wezenlijk belang voor de protonenbalans is. Bij het afleiden van depositienormen uit deze experimenten dient daarom de nodige reserve in acht genomen te worden.

Bij de depositieniveaus van de eerste decennia van deze eeuw was het voortbestaan van levensgemeenschappen in vennen die hun bijzondere waarde danken aan enige directe toevoer van voedingsstoffen mogelijk (Hoofdstukken 5 en 6). Voor vennen waaraan geen voedingsstoffen uit de omgeving worden toegevoerd kan een dergelijke uitspraak nog niet worden gedaan. Arts (1986) komt voor vennen met het oeverkruidverbond tot dezelfde conclusie. Zij betrok de toevoer van protonen door natte neerslag en de toevoer van potentiële aciditeit in de vorm van ammoniak en ammonium in haar berekeningen van depositieniveaus, maar beschikte over onvoldoende gegevens om de verzurende droge depositie van zwaveldioxyde en de bufferende invloeden van sulfaten en nitraten hierbij te betrekken.

Het is wenselijk in toekomstige (model)studies van de relatie tussen actuele en historische depositieniveaus en verzuring van vennen rekening te houden met laatstgenoemde componenten en het droogvallen van venbodems in droge zomers.

6 Actief beheer van vennen

Zonder bewust ingrijpen zal de reeds ver voortgeschreden convergentie van levensgemeenschappen naar het 'knolrus - Eunotia exigua - Staurastrum punctulatum - type' in geïsoleerde vennen onverminderd voortgaan. Dit type levensgemeenschap kan in de meeste gevallen worden ingeschaald in het laagste niveau van waterkwaliteitsdoelstellingen (basiskwaliteit) van het IMP Water (Rijkswaterstaat 1986). Strikt genomen voldoet het niet eens aan sommige eisen van dit niveau (te lage pH, geen vis aanwezig).

Bij het formuleren van waterkwaliteitsdoelstellingen voor vennen kan niet aan enkele randvoorwaarden worden voorbijgegaan, die in hoofdzaak worden bepaald door maatschappelijke ontwikkelingen. Hoewel de zure atmosferische depositie wellicht kan worden gereduceerd, is het niet aannemelijk dat deze zal terugkeren tot het niveau van een eeuw geleden. Daardoor zullen organismen die zijn gebonden aan een zeer laag mineralengehalte van het venwater niet terugkeren. Het is evenmin aannemelijk te veronderstellen dat er grote sommen gelds aan 'restauratie' van venecosystemen besteed kunnen worden. Voor een aantal vennen is misschien het middelste niveau haalbaar. Volgens het IMP Water (Rijkswaterstaat 1986) gaat dit in de richting van de natuurlijke toestand, maar is nog niet gelijk daaraan. Misschien is het beter om bij Nederlandse vennen van het middelste niveau te spreken bij zwak zure omstandigheden (pH 5-6), waarbij het mineralengehalte hoger is dan in vennen met dezelfde pH, maar zonder de invloed van zure depositie en/of voedselverrijking uit de omgeving.

Dergelijke toestanden zijn te creëren door actief beheer. In tegenstelling tot het gestelde in het IMP Water (Rijkswaterstaat 1986) zijn het nalaten van oogsten, uitzetten van organismen en ander gebruik niet noodzakelijk. Deze activiteiten zijn soms zelfs vereist. Daarbij verschijnen, naast soorten uit matig voedselarme tot matig voedselrijke situaties, meestal ook ook 'storingsindicatoren'. Deze wijzen op instabiele (metatrofe) omstandigheden. De 'fijnproevers' uit stabiele (mesotrofe) milieus verschijnen niet of nauwelijks. Dit laatste geldt vooral de sieralgen. Een aantal voorbeelden illustreert de mogelijkheden en beperkingen.

Waterlobelia komt nog voor in twee vennen, waar de minerale bodem door actief beheer wordt vrijgehouden van organisch materiaal. In het verleden werden deze vennen beïnvloed door toevoer van voedselrijk water van elders. Biesvaren komt nog voor in een ven, waaraan buffercapaciteit wordt toegevoerd in de vorm van urine van zwemmers en waaraan grondwater wordt toegevoerd (Arts e.a. 1986). In het laatste ven (META I in Hoofdstuk 2) waren in 1975 naast soorten kiezelwieren uit voedselrijk en voedselarm water ook soorten uit matig voedselrijk, zwak zuur water aanwezig. Dit was eveneens het geval in META II, dat ten behoeve van de sportvisserij bemest en bekalkt werd. Hofstra (1982) vond soorten uit het oeverkruidverbond in slootjes, vijvers en door zandwinning ontstane plasjes op voedselarme grond, waar voedselrijk water van elders werd aangevoerd. Kwakkestein (1980) vond bijzondere sieralgen op de plaats waar kalk- en voedselrijk water in een zuur ven sijpelde. Van Tooren & Van Tooren (1984) vermeldden een toename van sieralgen uit matig voedselrijk water na toevoer van grond- en oppervlaktewater naar het oorsponkelijk zure water van een ijsbaan.

In dit kader is waarschijnlijk samenwerking met hengelsportverenigingen mogelijk. Vanwege de armoede aan van nature visrijk oppervlaktewater van de voedselarme zandgronden zijn veel vennen in het verleden bekalkt en bemest. Uit ongepubliceerde gegevens van de Directie Visserijen van het Ministerie van Landbouw en Visserij blijkt dat de bekalkingen jaarlijks of zelfs nog frequenter werden verricht.

Onderzoek naar manieren waarop dergelijke zwak zure systemen beheerd en gecreëerd kunnen worden is van belang. Deze vorm van 'ecologisch tuinieren' mag niet dienen om het publiek kalk in de ogen te strooien, alsof het verzuringsprobleem door middel van eenvoudige natuurtechnische ingrepen kan worden opgelost. Voor de uiteindelijke oplossing van de verzuring van grond- en oppervlakte water, bossterfte en aantasting van cultuurgoederen door zure neerslag is een drastische reductie van de zure atmosferische depositie noodzakelijk.

7 Aanbevelingen voor verder onderzoek

1. Voortzetting van het monitoringsonderzoek van chemie, kiezelwieren en macrofyten in ten minste de drie tijdens dit onderzoek intensief bestudeerde vennen, zo mogelijk aangevuld met een ven dat in het verleden niet (noemenswaard) met voedingsstoffen is verrijkt.
2. Het opstellen van zwavel- en stikstofbalansen voor een aantal vennen gedurende een reeks van jaren met één of meer droge zomers.
3. Palaeolimnologisch en historisch onderzoek als in Hoofdstuk 6 in tien tot twintig geïsoleerde vennen om landelijk een representatief beeld van de geschiedenis van alkalinisering en verzuring te verkrijgen.
4. Modelleren van de verkregen tijdreeksen in relatie tot tijdreeksen van zure atmosferische depositie, om voorspellingen te doen over biologische en chemische veranderingen in vennen bij toekomstige veranderingen van zure atmosferische depositie.

5. Onderzoek naar kleinschalige, lokale maatregelen om in vennen een waterkwaliteit van het middelste niveau mogelijk te maken.
6. Onderzoek naar mogelijkheden om de windwerking in de omgeving van vennen en plaatsen waar vennen kunnen ontstaan te vergroten, b.v. door het kappen van bossen, verwijderen van bosopslag en het toepassen van begrazing.

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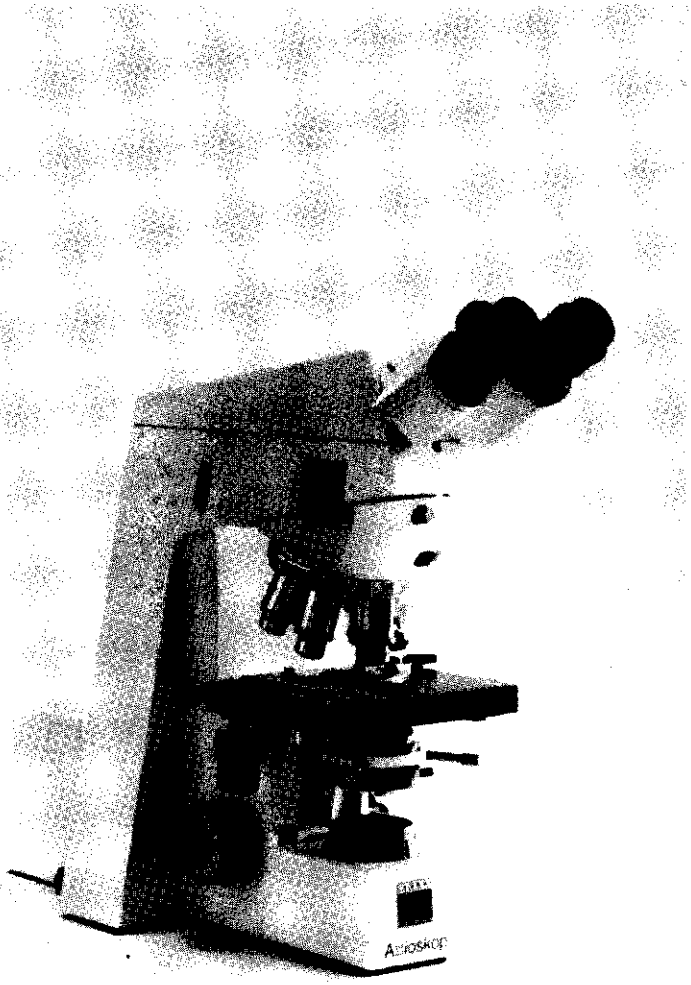

ZEISS Axioskop doorvallend licht microscoop voor biologisch en medisch onderzoek

SAMENVATTING

Hoofdstuk 1 bevat motivering, doelstelling en opzet van het onderzoek, naast een overzicht van ontwikkelingen in het plantkundig onderzoek van vennen vanaf ca 1900.

Bij de aanvang van dit onderzoek, in 1976, was over de invloed van zure atmosferische depositie (zure neerslag) op oppervlaktewateren in Nederland nauwelijks iets bekend. Er werd verwacht dat effecten van zure neerslag vastgesteld zouden kunnen worden, daar in gebieden met een veel geringere zure atmosferische depositie, zoals Scandinavië, de visstand van kalkarme, slecht gebufferde wateren al sinds de twintiger jaren terugliep als gevolg van verzuring door atmosferische depositie.

De belangrijkste groep van kalkarme, slecht gebufferde oppervlaktewateren in Nederland vormen de vennen. Deze plassen op voedselarme zandgrond worden geheel of grotendeels door de neerslag van water voorzien. Voedselarme en matig voedselarme vennen herbergen karakteristieke levensgemeenschappen en behoren tot de meest waardevolle natuurelementen in Nederland en omringende landen. Veel vennen hebben hun voedselarme en zwak zure karakter verloren door bemesting met landbouwwater, visserij, zwemmen enz. Betrekkelijk ongestoorde vennen zijn zeldzaam en komen bijna alleen nog in natuurreservaten voor. Er werd verwacht dat juist in deze vennen de gevolgen van verzuring het best waarneembaar zouden zijn.

Ter formulering van een beleid inzake de bestrijding van verzuring worden in dit onderzoek veranderingen in de chemie, met name de zuurgraad, van vennen beschreven op tijdschalen van eeuwen, decennia en jaren. Tevens wordt nagegaan welke natuurlijke en kunstmatige oorzaken voor deze veranderingen en de verschillen in zuurgraad tussen vennen verantwoordelijk zijn.

Directe waarnemingen van de chemische samenstelling van venwater zijn in het begin van deze eeuw weinig en in de vorige eeuw geheel niet verricht. Daarom worden gegevens over het voorkomen van macrofyten (hogere planten en mossen) en kiezelwieren in het verleden gebruikt als indicatoren voor de vroegere voedselrijkdom en zuurgraad. Veranderingen worden afgeleid door vergelijking van oude met recente inventarisaties.

In Hoofdstuk 2 wordt de toestand van vennen bij Oisterwijk getypeerd met geconserveerde planktonmonsters uit 1916-29 en 1975. De recente vegetatie van macrofyten wordt vergeleken met literatuurgegevens van omstreeks 1930. In het begin van deze eeuw waren er tussen deze vennen grote verschillen in zuurgraad en voedselrijkdom, veroorzaakt door de verschillende mate waarin ze door landbouwwater (directe inspoeling of via sloten) werden beïnvloed. Bij de recente inventarisatie treedt een tweedeling op (Hoofdstuk 2, Figuur 5): er resten slechts zeer voedselrijke, alkalische vennen (pH > 7) in landbouwgebieden en geïsoleerde, voedselarme, sterk zure vennen (pH < 4,5) in natuurreservaten. De verzuring wordt toegeschreven aan de invloed van zure neerslag. De oorspronkelijke variatie in levensgemeenschappen is hierdoor achteruitgegaan, waarbij vooral zeldzame soorten macrofyten en kiezelwieren zijn verdwenen. In vennen die door sportvisserij of zwemactiviteiten (niet overmatig) met voedsel zijn verrijkt, komen nog soorten uit matig zuur milieu (pH 5-6) voor, naast soorten uit sterk zuur en alkalisch water.

In Hoofdstuk 3 worden de veranderingen in kiezelwierencombinaties van zestien vennen tussen ca 1920 en 1978 in samenhang met de chemie van het water beschreven. Van deze vennen (bij Oisterwijk, Kootwijk en Dwingeloo) was niet bekend dat ze in deze eeuw door direct menselijk handelen zijn beïnvloed. De oude en recente kiezelwierencombinaties worden vergeleken door analyse van pH-spectra, diversiteit (verscheidenheid), dissimilariteit (af-

wijkendheid) en hoofdcomponentenanalyse (een statistische techniek om de samenhang tussen een groot aantal variabelen overzichtelijk te maken). Uit de pH-spectra blijkt dat de vroegere variatie tussen vennen met een laag humusgehalte van het water (pH 4-6) is teruggelopen in de recente monsters (pH 3,7-4,6). In vennen met humeus water is de pH (ca 4,5) niet significant veranderd. De diversiteit neemt significant af in niet-humeuze vennen en niet significant toe in humeuze vennen. De dissimilariteit neemt significant af in niet-humeuze vennen en verandert niet in humeuze vennen. De eerste hoofdcomponent verklaart 61% van de totale variatie tussen de monsters en wordt vrijwel geheel bepaald door Eunotia exigua. Deze soort komt ook voor in voedselrijke wateren met een hoog gehalte aan minerale zuren (b.v. afvalwater van ertsmijnen) en is nog nauwelijks gevonden in verzuurde wateren in Scandinavië. Dit wijst erop dat de Nederlandse vennen in biologisch opzicht in veel sterkere mate door verzuring zijn beïnvloed dan de Scandinavische meren.

De eerste hoofdcomponent is sterk positief gecorreleerd met de sulfaatconcentratie en andere factoren die samenhangen met verzuring (b.v. aluminium) en sterk negatief gecorreleerd met factoren die samenhangen met de aanwezigheid van humuszuren. Oude monsters uit alle vennen hebben lage en recente monsters uit niet-humeuze vennen hebben hoge scores op de eerste hoofdcomponent. De oorspronkelijke variatie, veroorzaakt door lokale oorzaken, heeft plaats gemaakt voor een variatie die wordt veroorzaakt door verschillen in sulfaatconcentraties. Naast zure depositie komen ook bebossing van de omgeving van vennen en het optreden van droogteperioden in aanmerking als oorzaak van toename van de sulfaatgehalten. Verschillen in sulfaatgehalte, en daardoor in pH, kunnen ook worden veroorzaakt door verschillen in sulfaatreductie, samenhangend met de beschikbaarheid van organische stof.

Het doel van het onderzoek van Hoofdstuk 4 is om de invloed van waterdiepte en droge zomers op verzuring van vennen te beschrijven en om aan te tonen dat vennen mede door hun ondiepte sterker verzuurd zijn dan meren in het buitenland. Dit onderzoek was geconcentreerd in drie vennen (Achterste Goorven, Gerritsfles en Kliplo), die verschillen in de mate van verzuring. Van deze vennen zijn relatief veel oude gegevens over macrofyten en pH en oude planktonmonsters beschikbaar. Het waterpeil, de chemische samenstelling van het water en de samenstelling van de kiezelwierencombinaties werden regelmatig gevolgd van 1979 tot 1985 en dieptekaarten werden vervaardigd.

In zeer droge zomers (b.v. 1921, 1947, 1959 en 1976) valt ongeveer 20% van bodem van Kliplo droog. In Gerritsfles en A. Goorven is dit respectievelijk ca 50 en 70%. In het humeuze ven Kliplo konden de relatief geringe biologische en chemische verschillen voor en na 1976 niet aan de droogte van dit jaar worden gerelateerd. In Gerritsfles en vooral in A. Goorven, met minder humeus water, waren de sulfaatconcentraties in 1977 en 1978 zeer hoog en namen daarna geleidelijk af. In deze twee vennen kwamen knolrus en Eunotia exigua de eerste jaren na de droogte van 1976 zeer veel voor en namen daarna weer af; het snelst in de Gerritsfles, waar de verblijftijd van het water (3 jaar) korter is dan in het A. Goorven (5-6 jaar), zoals blijkt uit een eenvoudig hydrologisch model. E. exigua reageert met vertraging.

Kennelijk werden tijdens de droogte van 1976 gereduceerde zwavelverbindingen, die zich in de decennia ervoor in de bodem hadden opgehoopt, geoxydeerd. Na het vollopen van de vennen was er in het water veel sulfaat (bij een lage pH), dat daarna afnam door sulfaatreductie en afvoer via drainage. De verhouding sulfaat/chloride is in venwater kleiner dan in regenwater, hetgeen wijst op sulfaatreductie. Door de produktie van alkaliniteit bij dit proces en bij denitrificatie steeg de pH op den duur weer.

De extreem droge zomer van 1921 had geen duidelijke invloed op de samenstelling van kiezelwiermonsters uit het A. Goorven. E. exigua was nauwelijks aanwezig. Kennelijk hadden zich in 1921 nog weinig gereduceerde zwavelverbindingen, afkomstig van atmosferische depositie, in het sediment van dit ven kunnen ophopen. In de Gerritsfles werd na de droge zomer van 1959 een sterke toename van E. exigua gevonden.

Sinds ca 1920 is de pH in Kliplo met ca 0,5 punt gedaald, in de andere twee vennen met 1-2 punten. Dit blijkt uit directe metingen en pH-schattingen met kiezelwieren. De veranderingen in Kliplo, waar de gereduceerde zwavelverbindingen in de bodem blijven opgeborgen, zijn vergelijkbaar met die in verzurende meren in Scandinavië en Noord-Amerika. In A. Goorven en Gerritsfles, waar de gereduceerde zwavelverbindingen bij ernstige droogten worden geoxydeerd, is de verzuring veel groter dan in genoemde meren.

Door paleolimnologisch onderzoek is gebleken dat verzuring van Schotse en Scandinavische meren al tussen 1850 en 1900 is begonnen. Hierbij werden restanten van organismen in het bodemmateriaal bestudeerd en gebruikt om een indruk te krijgen van het vroegere milieu. In Hoofdstuk 5 wordt verslag gedaan van een dergelijk onderzoek in het A. Goorven. Ondanks de verstorende invloed van verplaatsing van sedimenten door wind en dieren (bioturbatie), is het mogelijk om in de ondiepe vennen door middel van paleolimnologische methoden een redelijk beeld te krijgen van de vroegere milieuomstandigheden. Er is goede overeenstemming tussen directe pH-metingen uit verschillende perioden enerzijds en de pH-waarden die werden berekend uit de kiezelwieren uit verschillende laagjes van het sediment en uit planktonmonsters van verschillende perioden anderzijds. De datering geschiedde door analyse van lood-210, pollen, zaden en vruchten.

Hoewel het A. Goorven al in het Laat-Glaciaal ontstond, dateren de oudste sedimentlagen op de plaats waar werd geboord uit de vroege negentiende eeuw. Oudere sedimenten zijn waarschijnlijk door steken van turf verwijderd. Rond 1830 was de pH ca 5 en steeg tot ca 6 aan het begin van deze eeuw, door aanvoer van matig voedselrijk water uit het Voorste Goorven. Vermoedelijk kwam hier ca 1880 een einde aan door aanleg van een dam. Door deze aanvoer konden planten uit een niet extreem voedselarm, zwak zuur milieu als waterlobelia en teer vederkruid zich vestigen. Er kwamen zeldzame soorten muggelarven voor, die nooit levend in Nederland zijn aangetroffen en thans nog in Scandinavië voorkomen. Vervolgens is de pH afgenomen tot ca 4. De bijzondere plante- en diersoorten zijn verdwenen om plaats te maken voor een beperkte groep zuurtolerante organismen.

Hoofdstuk 6 gaat over een vergelijkbaar onderzoek in Gerritsfles en Kliplo. Er werd verwacht dat met name de Gerritsfles een eeuwen oud, 'ongestoord' ven zou zijn en dat hier vastgesteld zou kunnen worden wanneer waterverzuring in Nederland begonnen is. Uit combinatie van de gegevens van de boorkern met gegevens uit gepubliceerde en ongepubliceerde bronnen blijkt echter dat dit laatste ven pas in het begin van de negentiende eeuw als een humeuze, voedselarme plas is ontstaan uit een vochtig heideveld, door bodemkundige processen die te maken hebben met de nabijheid van stuifzand. Doordat jaarlijks ruim duizend schapen in het ven werden gewassen werd de Gerritsfles voedselrijker en steeg de pH van ca 4,5 tot ca 6 rond 1900. Er verschenen planten uit het oeverkruidverbond (waterlobelia, oeverkruid) en het water werd gebruikt als visvijver. Ook onder de micro-organismen nam de verscheidenheid toe. Nadat het wassen van de schapen in het begin van deze eeuw werd gestaakt en de zure neerslag toenam trad verzuring op, in verhevigde mate sinds ca 1950.

Het bekken van Kliplo was geheel opgevuld met voedselarm, zuur veen, dat in het begin van de vorige eeuw gedeeltelijk werd afgegraven. De ontstane

plas had een pH van ca 4,5, die steeg tot ca 6 omstreeks 1900. Deze stijging was het gevolg van een verrijking met voedsel. Vermoedelijk werd het ven in de vorige eeuw gebruikt als schapenwas en/of eendenkooi. Na 1900 daalde de pH geleidelijk tot ca 5.

De ontwikkelingen in de drie vennen sinds 1800 worden vergeleken met die in een verzurend Schots meer (Figuur 1 van Hoofdstuk 7). De vennen zijn veel dynamischer systemen dan dit meer en andere verzurende meren in Schotland, Scandinavië en Noord-Amerika. De zwak zure omstandigheden (pH 5-6) rond 1900 in de drie vennen zijn een gevolg van menselijk handelen. De daling van de pH na 1900 is deels het gevolg van het staken van voedselverrijkende activiteiten en deels van de toename van de zure depositie. Het is daarom niet mogelijk om te bepalen wanneer de verzuring door atmosferische depositie in deze vennen begon.

Het blijkt dat, ten minste in het intensief gecultiveerde landschap van West-Europa, historische informatie over menselijke beïnvloeding van de bestudeerde wateren en het omringende landschap noodzakelijk is om juiste conclusies omtrent de oorzaak van vastgestelde verzuring te kunnen trekken.

In Hoofdstuk 7 worden de oorzaken van zuurgraadverschillen in ruimte en tijd samengevat. Natuurlijke verschillen worden o.a. door de aard van de bodem, de vorm en diepte van het waterbekken en de samenstelling van de neerslag bepaald. Antropogene verschillen worden vooral veroorzaakt door bemesting en zure neerslag. Doordat de menselijke beïnvloeding in het verleden op bescheiden schaal plaatsvond werd de verscheidenheid van de levensgemeenschappen binnen en tussen vennen hierdoor bevorderd. Door heideontginningen zijn veel vennen overmatig met voedsel verrijkt en gingen de karakteristieke, thans zeldzame, soorten planten en dieren uit voedselarm tot matig voedselarm water sterk achteruit. Zij vonden een refugium in geïsoleerde vennen in natuurreservaten, waar zij door verzuring verder achteruitgingen. De verzuring is zowel het gevolg van zure neerslag als van het verdwijnen van oude agrarische gebruiksvormen, zoals het wassen van schapen en het roten van vlas. Het verdwijnen van begrazing door schapen en de bebossing van heiden en stuifzanden in de omgeving van geïsoleerde vennen veroorzaakten een vermindering van een geringe mate van dynamiek, met name windwerking. Dit droeg waarschijnlijk bij tot de achteruitgang van een aantal karakteristieke venplanten die van deze dynamiek afhankelijk waren. Tevens werden de ontstaansmogelijkheden voor nieuwe vennen in en nabij stuifzandgebieden door deze verstarring van het landschap verminderd.

Uitgaande van de criteria verscheidenheid en onvervangbaarheid worden biologische normen voor de beoordeling van vennen geformuleerd. Zolang de zure atmosferische depositie nog niet op het niveau van het begin van deze eeuw terug is, kan in een aantal vennen aan deze normen wellicht worden voldaan door een lokale, bescheiden toevoer van bufferstoffen. Hierdoor kan een zwak zuur milieu worden gecreëerd, waar een aantal soorten uit het pH-interval 5-6 kan voorkomen, maar waar de meest veeleisende soorten ontbreken.

Tenslotte wordt aanbevolen om door te gaan met het verzamelen van materiaal voor historische en recente biologische en chemische tijdreeksen in een aantal vennen en dit te gebruiken voor het opstellen van modellen om uitspraken te kunnen doen over de effecten van toekomstige veranderingen van de zure depositie. Om inzicht te krijgen in de chemische processen die zich bij verzuring van vennen voordoen, is het opstellen van zwavel- en stikstofbalansen van een aantal vennen over een reeks van jaren dringend noodzakelijk. De mogelijkheden om de windwerking in de omgeving van vennen, waar sommige karakteristieke planten van afhankelijk zijn, te vergroten, verdienen nader onderzoek.

SUMMARY

Chapter 1 deals with the rationale, aim and research approach of the investigations. A survey of the botanical investigations in moorland pools in The Netherlands since 1900 is presented too.

In 1976, when the present investigations started, almost nothing was known about the impact of acid atmospheric deposition ('acid precipitation') on surface water in The Netherlands. As acidification of weakly buffered surface waters due to acid precipitation has been observed in much more remote areas it was expected that this phenomenon could be observed in The Netherlands too.

Moorland pools ('vennen') are the most important group of weakly buffered surface waters in The Netherlands. They are situated in areas with oligotrophic, sandy soils and are entirely or mainly fed by precipitation water. A rare and characteristic flora and fauna is found in oligo- and mesotrophic moorland pools. Therefore they belong to the most valuable sites of nature in Western Europe. Many moorland pools have been eutrophied and alkalized due to nutrient enrichment by agricultural drainage water, fisheries, bathing etc. Relatively pristine moorland pools are rare and confined to nature reserves. It was expected that acidification could be observed particularly in the latter pools.

To provide data for policy-making in the field of abatement of acidification this thesis describes changes in chemistry, and particularly acidity of moorland pools on time scales of centuries, decades and years and tries to find explanations for the observed changes in the course of time and for the differences in acidity between moorland pools.

Direct observations of the chemical composition of moorland pool water were rarely made at the beginning of the 20th century and are unknown from the 19th century. Therefore, diatoms in old and recent samples and historical and recent data about the presence of aquatic macrophytes are used to infer changes in trophic state and acidity.

In Chapter 2 plankton tow diatoms from moorland pools near Oisterwijk from 1916-29 are compared with those from 1975. Recent inventories of macrophytes are compared with those from c. 1930. At the beginning of this century, a wide array of trophic state levels and acidities was found in the different pools, due to differences in the amount of nutrients, supplied by agricultural drainage water. During the recent inventories a bipartition was observed in hypertrophic, alkaline pools, situated in agriculture areas, and isolated, oligotrophic, very acid pools (pH < 4.5), situated in nature reserves (Ch. 2, Fig. 5). The acidification was attributed to acidification by acid atmospheric deposition. The variation in biocommunities decreased strongly over the period of half a century. Particularly rare macrophytes and diatoms declined. Taxa from weakly acid (pH 5-6) water still occurred in those pools which were (not excessively) enriched with nutrients by fisheries or excrements of swimmers, together with acidobiontic and alkaliphilous taxa.

In Chapter 3 old (c. 1920) and recent (1978) diatom assemblages from sixteen moorland pools in different parts of The Netherlands are compared by analysis of pH-spectra, diversity, dissimilarity and principal component analysis. The pH-spectra of clear water pools indicate that the formerly wide range of pH (4-6) is narrowed to 3.7-4.6 in the recent samples. No significant change of pH (c. 4.5) is seen in the brown water pools. Diversity declines significantly in clear water pools and increases insignificantly in brown water pools. The dissimilarity decreases in clear water pools, no change is found in brown water pools. The first principal component (PC 1) explains 61% of total variance between samples and is nearly completely determined by

Eunotia exigua, an acidobiontic diatom, which is also known from acid mine waters. PC 1 has a strong positive correlation with sulphate and other factors related to acidification (e.g. aluminium) and a negative correlation with factors characterizing humic acid waters. Old samples have low scores on PC 1 and recent samples from clear waters have high scores on PC 1. The variation that was due to local factors in the old samples has been substituted by a sulphate controlled variation in the recent samples. The recent differences in sulphate concentrations and pH of the pools, e.g. sulphate reduction, drought and afforestation of the surrounding landscape, are discussed.

A hypothesis that depth distribution and the occurrence of extremely dry years play a role in the acidification of moorland pools and that moorland pools are more severely acidified than lakes, due to their shallowness, is tested in Chapter 4. The research was conducted in three pools (Achterste Goorven, Gerritsfles and Kliplo), which differed in the extent of acidification, as was revealed in the preceding chapter. Relatively many old data concerning macrophytes and pH and old plankton tow samples from these sites are available. Water level, water chemistry and the composition of diatom assemblages were monitored from 1979 through 1984 and bathymetry was mapped.

In extremely dry summers (e.g. 1921, 1947, 1959 and 1976) in Kliplo, Gerritsfles and Kliplo about 20, 50 and 70% of the bottom respectively is exposed to the atmosphere. In the brown water pool Kliplo the relatively small chemical and biological differences before and after 1976 could not be attributed to the drought of that year. In the clear water pools Gerritsfles and particularly A. Goorven sulphate concentrations were extraordinary high in 1977 and 1978 and decreased afterwards, parallel to the abundance of Juncus bulbosus. E. exigua decreased with a delay. The decrease was most rapid in Gerritsfles, which has a shorter water residence time (3 years) than A. Goorven (5-6 years), as was inferred from a simple hydrological model.

During the dry spell of 1976, the reduced sulphur compounds, which accumulated in the sediments during the preceding decades, were oxidized and caused pH-values below 4. Sulphate was released into the water when the water level rose, and decreased by overflow of the pool. Also sulphate must have been disappeared by sulphate reduction, because at an average the ratio of sulphate to chloride is lower in pool water than in precipitation water. Later on the pH increased above 4, presumably because of alkalinity production by sulphate reduction and denitrification.

From A. Goorven a series of plankton tow diatom samples from the period 1916-1929 was analysed. E. exigua was hardly present and the drought of 1921 did not affect the composition of the diatom assemblages clearly. Apparently no reduced sulphur compounds, derived from atmospheric deposition, had accumulated in the sediments at that time. In Gerritsfles E. exigua increased after the dry summer of 1959.

In Kliplo the pH has declined by c. 0.5 unit over the last six decades, as appears from direct measurements and inference from diatoms. The changes in Kliplo, where the reduced sulphur compounds are stored permanently in the sediments, are similar to those in acidifying lakes in Scandinavia and North America. In A. Goorven and Gerritsfles the pH decreased by 1-2 units. The more severe acidification of these pools is at least partly due to the exposure of the sediments in extremely dry summers.

It has been shown by palaeolimnological methods that acidification of lakes in Scotland and Scandinavia started between 1850 and 1900. Such methods might be used to determine the onset of acidification in The Netherlands, but in shallow pools the sedimentation process is more intensively disturbed by wind mixing, bioturbation and desiccation in dry summers than in lakes. It appears from Chapter 5 that the acidification history of A. Goorven can be

reconstructed rather well by sediment core studies, as sediment diatom inferred pH values agree reasonably well with plankton tow diatom inferred pH-values and direct measurements of pH. The sediments were dated by analysis of Pb-210, pollen, seeds and fruits.

Although A. Goorven was formed in the Late Glacial period, the oldest sediments at the coring site were from the early 19th century. Older deposits have been removed by peat digging. Around 1830 the pH was c. 5 and increased to c. 6 in the early 20th century, due to inflow of mesotrophic water from the pool Voorste Goorven. The inflow stopped when a dam was constructed between the two pools, presumably around 1880. Because of the nutrient enrichment oligo-mesotraphent species (e.g. Lobelia dortmanna, Myriophyllum alternifolium) settled. Chironomids of the Cladopelma-assemblage, which have never been reported alive from The Netherlands, and are more typically found in Scandinavian soft water lakes, were present. Subsequently the pH decreased to current levels of c. 4 and most rare plants and animals have disappeared and were replaced by a limited number of acid-tolerant taxa.

Similar research in Gerritsfles and Kliplo is described in Chapter 6. When this project started it was expected that particularly Gerritsfles would be a comparatively old and 'undisturbed' moorland pool, where the onset of acidification of moorland pools in The Netherlands could be determined. However, after combining palaeolimnological data and documented evidence it appeared that the latter pool originated from a humid heath as late as the early 19th century. It was formed as a shallow, oligo-dystrophic pool (pH c. 4.5) due to pedological processes, associated with the presence of aeolian drift sand. The pool was enriched with nutrients, because over thousand sheep were washed in the pool each year and the pH increased to c. 6. Littorellion species (Littorella uniflora, Lobelia dortmanna) settled and the pool was used as a fish pond. The diversity of micro-organisms increased too. Sheep washing finished around 1900 and the pool started to acidify, particularly after 1950, parallel with the increase of acid atmospheric deposition.

The oligotrophic peat-bog of Kliplo was partly excavated in the beginning of the 19th century. The pH of the pool was c. 4.5 and gradually increased to c. 6 in 1900, due to eutrophication, presumably because of sheep washing or use of the pool as a duck-decoy. After 1900 the pH decreased to current levels of c. 5.

In Fig. 1 of Chapter 7 the changes of pH in the three pools since 1800 are compared with those in an acidifying Scotch lake, which is an example for acidifying lakes in Northern Europe and Northern America. The moorland pools are more dynamic systems than these lakes. The weakly acid conditions (pH 5-6) around 1900 are anthropogenic. The decrease of pH in the present century is due both to termination of direct nutrient enrichment of the pools and of increased acid atmospheric deposition. Consequently it is hard to determine when acidification by acid atmospheric deposition started.

Documented evidence of human influence upon the study sites, combined with palaeolimnological techniques is found to be necessary to obtain proper conclusions with studies on the history of surface water acidification.

The causes of pH-differences in space and time are summarized in Chapter 7. Natural pH differences are due to depth distribution and soil conditions, composition of precipitation etc. Anthropogenic differences are caused by nutrient enrichment and acid atmospheric deposition. In the past the human influence was less intensive than at present and promoted the diversity within and between moorland pools. Many pools were drained or excessively enriched with nutrients because of the reclamation of heathlands after 1900. Consequently the characteristic, presently rare, species from oligotrophic to mesotrophic water bodies declined and became confined to isolated pools in

nature reserves, where acidification caused a further decline. The acidification of moorland pools is due both to the disappearance of traditional agricultural activities (sheep washing, retting of flax etc.) and to the increase of acid atmospheric deposition. The disappearance of sheep grazing and the afforestation of heathlands near isolated moorland pools caused a decrease of wind induced dynamics. This decrease probably contributed to the decline of plants which were dependent on these dynamics. Also the formation of new moorland pools in and near areas of aeolian drift sand is hampered in a fixated landscape.

Biological standards for the assessment of water quality in moorland pools are formulated, based on the criteria diversity and irreplaceability. A weakly acid environment can be created deliberately by a local and moderate supply of buffering substances to acidified moorland pools. This permits a number of species from the pH-interval 5-6 to live, with notable exception of the most sensitive and rare ones, which are particularly found in water with very low concentrations of ions. Such an intervention is necessary in some pools to achieve the formulated standards, as long as the acid atmospheric deposition has not reached the level of the beginning of this century.

Finally it is recommended to continue chemical and biological monitoring in a number of pools and to use the data for modelling the impact of acid atmospheric deposion on chemical and biological conditions in moorland pools, to predict the effects of future changes of acid atmospheric deposition on moorland pools. For this purpose it is also necessary to calculate sulphur and nitrogen budgets from a series of consecutive years, including dry ones, for a number of moorland pools. The possibilities to enhance wind induced dynamics near moorland pools, an important environmental factor for some characteristic plant species, are worth to be investigated.

VERANTWOORDING

De determinaties en tellingen van kiezelwieren van Hoofdstuk 2 zijn geheel voor de verantwoordelijkheid van H. Kooyman-van Blokland, alle overige aspecten voor die van H. van Dam.

Soortbepaling en telling van de kiezelwieren van Hoofdstuk 3 vonden plaats onder dagelijkse begeleiding van H. van Dam door G. Suurmond, die ook een begin maakte met de statistische analyse. C.J.F. ter Braak en Ir J. Oude Voshaar zijn in de eerste plaats verantwoordelijk voor de keuze van de statistische methoden. Alle overige aspecten komen voor rekening van H. van Dam.

De opzet van het onderzoek van Hoofdstuk 5 en het historisch onderzoek werden verzorgd door H. van Dam. De determinaties en tellingen van kiezelwieren uit sedimenten werden, in nauw overleg met H. van Dam, verricht door dr M.D. Dickman, die ook diverse concepten van dit hoofdstuk redigeerde. C.N. Beljaars telde de kiezelwieren uit planktonmonsters, onder verantwoordelijkheid van H. van Dam. Voor uitvoering, interpretatie en rapportage van de aspecten pollen (inclusief vruchten en zaden), muggelarven (Chironomidae) en looddatering zijn respectievelijk dr B. van Geel, ir A. Klink en A. van der Wijk verantwoordelijk. H. van Dam verzorgde de eindredactie. De verantwoordelijkheden voor dit hoofdstuk zijn soms moeilijk te scheiden, vanwege de veelvuldige discussies tussen de auteurs.

De opzet van het onderzoek van Hoofdstuk 6 komt voor rekening van H. van Dam, evenals het historisch onderzoek, de integratie van de resultaten van de deelonderzoekingen en het schrijven van het artikel. C.N. Beljaars en A. Mertens determineerden en telden de kiezelwieren onder begeleiding van H. van Dam. Dr B. van Geel voerde de pollen-, vruchten- en zadentellingen uit, interpreteerde de resultaten hiervan en stelde de indeling in zones op. Dr J.F.M. Geelen en R. van der Heijden determineerden en telden de watervlooien (Cladocera) en interpreteerden de resultaten hiervan. A. van der Wijk is verantwoordelijk voor de looddateringen.

De verantwoordelijkheid voor de Hoofdstukken 1, 4 en 7 berust geheel bij H. van Dam.

CURRICULUM VITAE

De auteur werd geboren op 8 november 1947 te Amsterdam en volgde het lager- en middelbaar onderwijs te Velsen, waar in 1965 het diploma H.B.S.-B werd behaald.

Hij legde het propedeutisch examen Natuurkunde af in 1966 aan de Universiteit van Amsterdam. Aan dezelfde Universiteit werd in 1970 het kandidaatsexamen Biologie (Bl) afgelegd. Het doctoraaldiploma Biologie werd behaald in 1973, met als hoofdrichting Bijzondere Plantkunde (prof. dr A.D.J. Meeuse). Onder begeleiding van dr P.F.M. Coesel werd onderzoek verricht naar epifytische kiezelwieren van het Naardermeer, in relatie tot watervervuiling. Voor het Bijvak Plantenfysiologie (prof. dr D. Stegwee) werd een onderzoek verricht naar bloei-inductie van Lemnaceae, o.l.v. dr G.J.H. Bennink. Aan de Rijksuniversiteit te Leiden werden voor het bijvak Theoretische Biologie (prof. dr M. Jeuken) o.l.v. drs E. Meelis hoofdstukken uit de Mathematische Ecologie bestudeerd.

Na het doctoraalexamen was hij van 1973 tot 1975 werkzaam als ecoloog bij het Rijksinstituut voor Drinkwatervoorziening te 's-Gravenhage, waar hij, gedetacheerd bij het Rijksinstituut voor Natuurbeheer te Leersum, deelnam aan een interdisciplinaire studie over gevolgen van infiltratie van voorgezuiverd Rijnwater op de Veluwe.

In 1976 volgde de aanstelling als hydrobioloog bij het Rijksinstituut voor Natuurbeheer, waar het onderzoek voor dit proefschift werd verricht, naast deelname aan multidisciplinaire landschapsecologische onderzoekprojecten.